THE ROLE OF THE COCOONS OF ORB-WEAVING SPIDERS

By

CRAIG S. HIEBER

A DISSERTATION SUBMITTED TO THE GRADUATE SCHOOL OF THE
UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1984

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the many friends and colleagues who aided me in this work. My major professor, John F. Anderson, has been a source of stimulation and encouragment. His comments on my work were always critical but fair, and he always emphasized the importance of doing good, solid research. Most importantly, he encouraged me to be as independent as possible while doing my research. To John I extend my sincerest thanks. The other members of my dissertation committee, Lincoln P. Brower, Jonathon Reiskind, and Reese I. Sailer, and the additional colleague, David H. Evans, who sat at my defense, all provided ready assistance during the research phase and many helpful editorial suggestions, from which I benefitted. I also recognize the advice or equipment provided by Drs. L. Berner, P. Feinsinger, M.H. Greenstone, F.J. Maturo, and B.K. McNab.

I was also fortunate to have the cooperation of a number of people in positively identifying my egg predators. Thanks for this service go to H. Townes (ichneumonids), American Entomological Institute; Dr. M.E. Schauff (eulophids), Systematic Entomology Lab, USDA; and Dr. L. Stange (mantispids), Division of Plant Industries, FDACS. Further thanks go to Mr. and Mrs. H.M. Chitty, who generously allowed me access to the Stardust Ranch for many of my experiments. I also acknowledge the Department of Zoology, Sigma

Xi, The Research Society, and the Florida Entomological Society for their generous financial support during my graduate program.

Numerous other post doctoral associates and graduate students in the Zoology Department have listened to my ideas and provided helpful suggestions. Among these I would especially like to thank J.B. Anderson, W.W. Henneman, J.R. Lucas, S.B. and B.J. Malcolm, P.G. May, M.S. Obin, K. Prestwich, N.E. Stamp, and N.T. Wheelwright. I also extend my thanks to A.D. Austin and K.E. Redborg for providing me with relevant manuscripts concerning my research.

I would like to separately thank my office mate and friend James A. Cohen (UVPD) for the countless stimulating discussions concerning my work and biology in general, the lovebug collaboration, and, in particular, for his influence on my writing. Jim, the "big chair" will always be open!

I would also like to separately thank Sherry M. Hieber for putting up with the late nights, the wild talk, and the oftentimes crazed behavior of this researcher. I could not have done this without her support and love.

Finally, I would like to thank my parents, Bernie and Doris Hieber, who have always told me I could be anything I wanted to be.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

THE ROLE OF THE COCOONS OF ORB-WEAVING SPIDERS

By

Craig S. Hieber

December, 1984

Chairman: John F. Anderson
Major Department: Zoology

The cocoons of spiders are believed to function in protecting the enclosed eggs and spiderlings from a number of biotic and abiotic factors. It has also been suggested that the wide diversity in cocoon architecture is the result of a "coevolutionary arms-race" between spiders and predators of their offspring. However, few studies have provided evidence to support these claims. This study provides evidence for some of these suggested functions by comparing the abilities of the cocoons of Mecynogea lemniscata and Argiope aurantia to control or limit temperature extremes, dessication, and attack by fungi and predators.

Results indicate that the cocoon of M. lemniscata limits dessication and fungal attack on the spiderling stage. In contrast, the cocoon of A. aurantia does not. Both cocoons probably play a

limited role in controlling temperature extremes from short-term radiant loads.

The cocoons of both species play a significant role in protecting the eggs and spiderlings from generalist and specialist predators. The association between the various layers making up these cocoons, and the specific methods used to gain entrance by their predators strongly supports the notion of a co-evolved system. However, the multiple functions of many cocoon components suggest the architectural details have probably resulted from diffuse evolutionary pressure from a number of simultaneously operating factors, instead of as counter-adaptations to specific predators.

In general, these results support many of the previous suggestions concerning cocoon function. Although specific functions are related to specific components within the cocoon, there can be great interspecific variation with relation to cocoon size and the relative sizes or thicknesses of the component parts of the cocoon. In addition, factors such as the size of the egg mass, the ultrastructure of the eggs, the habitat used for oviposition, the position of the cocoon within the habitat, and the reproductive behavior of the spider may also influence the ability of any part of the cocoon, or the whole structure, to limit the effects of any or all of the suggested factors affecting egg and spiderling survival.

CHAPTER I
INTRODUCTION

All spiders place their eggs in some form of silken cocoon (Turnbull 1973). For some, the cocoon is a relatively simple structure consisting of a few threads (e.g., the Pholcidae) and is used to move the egg mass about the web. In others, the cocoon provides a more complete container for carrying the eggs while hunting (e.g., the Lycosidae) or an additional level of protection for spiders which actively guard their eggs (e.g., the Oxyopidae). For many web-building spiders (e.g., the Araneidae), the cocoon is an elaborate structure composed of a variety of layers and is suspended in the habitat by different devices (McCook 1890, Scheffer 1905, Kaston 1948, Turnbull 1973). In many araneids where active care is non-existent, the cocoon represents the sum total of maternal care given to the eggs and spiderlings by the female.

Many web-building spiders deposit large clutches of eggs (Kaston 1948, Foelix 1982). Within the cocoon, the eggs undergo embryonic development, hatch to the deutova stage, and molt to the spiderling stage. The spiderlings can spend as long as 6 to 10 months in the cocoon overwintering until emergence in the spring (Anderson 1978). This long time interval, the large clutch sizes, and the absence of active maternal care have led to many suggestions concerning the function of cocoons. These include providing physical support for the egg mass (Christenson and Wenzl 1980),

protecting the enclosed eggs and spiderlings from thermal extremes (McCook 1890, Kaston 1948, Turnbull 1973, Gertsch 1979), dessication (Foelix 1982), fungal attack (Christenson and Wenzl 1980), drowning (Reichert 1981), UV light (Yoshikura 1969), and predator and parasite attack (Moore 1977, Austin and Anderson 1978, Robinson 1980, Austin, In press). Few studies, however, have examined the cocoons' effectiveness in controlling these factors.

I present here the results of several studies bearing on the functional roles that the cocoons of Mecynogea lemniscata (Walckenaer) and Argiope aurantia Lucas (Araneidae) play in protecting eggs and spiderlings from a number of biotic and abiotic factors. I also present results on the significance of cocoon timing and spacing, and how they interact with cocoon architecture to reduce predation. Both of these spiders use cocoons with dense covers (as opposed to the flocculent silk cocoon used by other araneids). However, they inhabit different environments, construct cocoons of different size and complexity, produce differing numbers of clutches, reproduce at different times of the year, and are attacked by different parasites. These differences are discussed in detail in Chapter II.

In Chapter III, I examine the role that cocoons, and in particular the flocculent silk layer within many cocoons, play in controlling temperature extremes. Many authors have suggested that the flocculent silk layer acts as insulation (McCook 1890, Kaston 1948, Turnbull 1973, Gertsch 1979). Published reports on this function have been contradictory. Schaefer (1976) reported that

the cocoons of Floronia bucculenta (Clerck) (Linyphiidae) protect the eggs from daily changes in ambient temperature. In contrast, Austin and Anderson (1978) concluded that the flocculent silk cocoon of Nephila edulis (Koch) (Araneidae) does not do so.

Chapter IV presents a comparative analysis of the capabilities of the cocoons of A. aurantia and M. lemniscata to control water loss. Although this is commonly assumed to be one of their major functions (e.g. Bristowe 1941, Foelix 1982), the data supporting this view are contradictory. Schaefer (1976) showed that the cocoon of F. bucculenta effectively controlled water loss from diapausing eggs. However, Austin and Anderson (1978) demonstrated that the flocculent silk cocoon of N. edulis had no effect on egg hatching success. Casual observations by McEwon (1963) suggest that the cocoon of an Australian Nephila species limits spiderling desiccation.

Closely related to the problem of desiccation is the problem of excess water which, if allowed to enter the cocoon, could dissolve materials from the surface of the eggs and increase their susceptibility to disease (Austin and Anderson 1978). Water entering the cocoon could also carry pathogens (Christenson and Wenzl 1980) or could drown the eggs or developing spiderlings. Although Reichert (1981) strongly suggests that the cocoons of Agelenopsis aperta (Gertsch) (Agelenidae) protect eggs from flooding, only Schaefer (1976) and Austin (1984) have demonstrated such a role for a cocoon or brood nest, respectively. In Chapter V, I compare the abilities of the cocoons of M. lemniscata and

A. aurantia to control the entrance of excess water and to limit fungal attack.

In Chapter VI, I examine the architecture of the cocoons of M. lemniscata and A. aurantia and its relation to the control of predator and parasite attack. Although considered one of the primary roles of cocoons (Austin and Anderson 1978, Robinson 1980, Austin, In press), this function has not been examined for any spider.

Many parasites locate their hosts in a stepwise manner using a variety of chemical and physical cues (Salt 1935, Vinson 1975, 1976). A number of biotic and abiotic factors have been suggested as disrupting these cues, thereby affecting the success of the parasites (Hassell 1971, Hassell and May 1973, Vinson 1976, Morrison and Strong 1980, Stiling and Strong 1982). However, host behaviors such as the phenology of emergence and their effects on the temporal and spatial distribution of the host have not often been considered as factors affecting parasite success. In Chapter VII, I examine the seasonal timing of reproduction, the length of the reproductive season, the timing of cocoon production, and the resulting spatial and temporal distribution of cocoons as methods used in conjunction with cocoons to interrupt the foraging behavior of egg predators.

Chapter VII summarizes my major results and discusses their relevance to the architecture of cocoons and to the diversity of reproductive tactics displayed by orb-weaving spiders.

CHAPTER II
THE EXPERIMENTAL ANIMALS, THEIR COCOONS, AND THEIR HABITATS

Mecynogea lemniscata (Walkenaer), the Basilica Spider

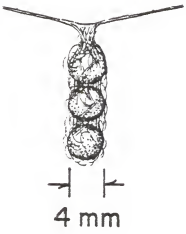
In northern Florida (at my study sites), M. lemniscata emerges in late March. Males mature in May and are found on the webs of females from early June to early July. The females mature in late May. Oviposition starts in mid-June and extends to mid-August with a peak in mid-July. Females disappear from their webs by late August.

The eggs of M. lemniscata take 16 days to eclose to the deutoval stage at 25°C and 70% RH. The deutoval stage lasts 4 days until the molt to the first instar spiderling stage (Hieber 1984). The spiderlings remain in the cocoon through the late summer, fall, and winter, and emerge in mid- to late March the following year after spending approximately 290 days in the cocoon (Anderson 1978).

The webs of M. lemniscata are placed in the shrub layer of deciduous forests, approximately 1-2 m above the ground. The cocoons are deposited at the web site, suspended above the domed orb-web from a single support line (Fig. 2-1a). The cocoons are produced sequentially, and the strings may contain 1-10 cocoons ($\bar{X}$ = 3.1 cocoons, SD = 1.6, n = 38). The individual cocoons are small (3-4 mm dia.) (Fig. 2-1b), and contain 8-30 eggs ($\bar{X}$ = 13.5 eggs, SD = 6.3, n = 35) (Hieber 1984). The cocoon covering is olive-green in

A.

B.



C.

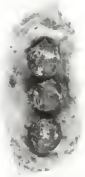


Fig. 2-1. A string of Mecynogea lemniscata cocoons suspended in the vegetation (A), showing the relative size of the cocoons (B), and with the external layer of silk peeled away to show the individual cocoons underneath (C). The external layer of silk is composed of old orb-webs applied to the cocoon string by the female spider. This layer also contains detritus and prey remains.

color, extremely hard, and tightly woven. Internally, there is a thin flocculent silk layer between the loose, non-agglutinated mass of eggs and the cocoon cover. The eggs are not enclosed in a membranous silk bag. The cocoons in a string are periodically covered with the damaged orb-web when it is replaced by the spider, giving the cocoon string an additional layer of loose dirty grey silk, detritus, and prey remains (Fig. 2-1c).

The eggs in M. lemniscata cocoons are attacked by two principal predators, the neuropteran Mantispa viridis Walker (Mantispidae) and the hymenopteran Tetrastichus sp. (Eulophidae) [near T. banksii Howard; see Hieber (1984)]. The eggs and spiderlings may also occasionally be attacked by ants, particularly if the support line breaks and the cocoons contact nearby vegetation or fall to the ground.

Mecynogea lemniscata is found in the shrub layer of southern deciduous forests (Levi 1980). In Florida, this spider prefers mesic hammocks, but can occasionally be found in more open habitats such as upland woods. In its preferred habitat, the humidity remains relatively constant (75-85% RH) during June and July (the egg laying and molting period) due to the overhead vegetation. From August on, the habitat dries and the RH may fall to 50% between rains. During the fall and winter, RH may fall as low as 30-40%. The temperature in this habitat is somewhat buffered due to the overhead vegetation which blocks the sun and it remains relatively constant (25-29° C) during the summer. From fall on, the temperature in the habitat follows the ambient temperature closely.

Argiope aurantia Lucas, the Black and Yellow Garden Spider

In northern Florida (at my study sites), male A. aurantia mature in July and are seen on the webs of females from approximately mid-July to mid-August (see Levi 1968). Females mature in late July to August (see Levi 1968). Oviposition starts in early August and continues to October, with the greatest number of clutches laid in mid-August to mid-September. Females disappear from most study sites by late October.

Development to the deutoval stage (eclosion) takes approximately 20-25 days in the laboratory at 25° C and 70-100% RH (see also Anderson 1978, Riddle and Markezich 1981). The deutoval stage lasts approximately 6 days before the molt to the pigmented first instar spiderlings. These spiderlings remain in the cocoon until late April or early May of the following year when they emerge.

Argiope aurantia builds its webs primarily in old field vegetation, or in the vegetation at field edges. Its cocoons are large brown spheres, 1-2 cm in diameter. Females deposit their cocoons singly, away from the web site, suspended in the vegetation 0.5 to 4.0 m above the ground by a cloud of fine support lines originating from "minute conical or pyramidal deltas" on the cocoon surface (McCook 1890; pg. 75) (Fig. 2-2a). The cocoons are multi-layered (Fig. 2-2b). The outer covering is usually composed of a thin, stiff, parchmentlike material with a glazing applied to it (almost like fiberglass), although it may occasionally be made of

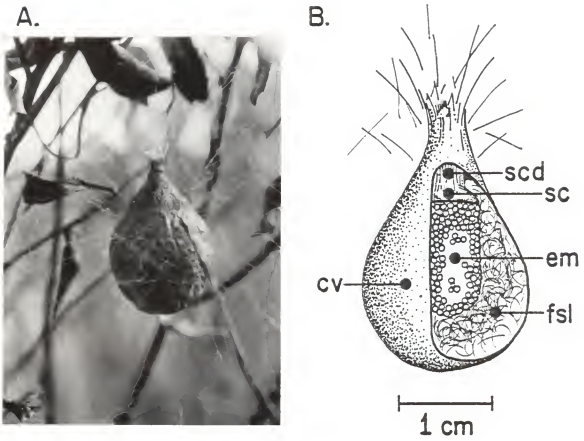


Fig. 2-2. The cocoon of Argiope aurantia suspended in the vegetation (A), and in cut away view (B) showing the position of the egg mass (em), silk cap (sc), silken cone and cord (scd), and flocculent silk layer (fsl) within the cocoon cover (cv).

a soft, thick, feltlike material. The agglutinated egg mass of 800-2000 eggs ($\bar{X}$ = 978.7 eggs, SD = 419.2, n = 40) is suspended within the cocoon from a thick silk cup, which in turn is attached to a cone and cord of strong silk which fills the stalk of the cocoon. The egg mass is covered by a fine membranous layer of silk, and is separated from the cover by a thick flocculent silk layer (see McCook 1890, pp. 79-80 for a complete description of the internal structure of the cocoon).

The eggs and spiderlings in A. aurantia cocoons are attacked by a number of general and specialized predators including the hymenopterans Trornatobia ovivora rufopectus (Cresson) (Ichneumonidae) (Cresson 1870, Keobele 1887, McCook 1890, Howard 1892, Champlain 1922, Enders 1974, Tolbert 1976), Pimpla aquilonia aquilonia (Cresson) (Ichneumonidae) (Davidson 1896), Chrysocharis banksii and Chrysocharis pikei (Entodontimidae) (McCook 1890), and Pediobius wilderi (Howard) (Entodontimidae) (McCook 1890) [this is probably a hyperparasite attacking T. ovivora rufopectus]; the dipterans Pseudogaurax signata (Loew) (Chloropidae) (Coquillet 1898), Pseudogaurax anchora (Loew) (Kaston and Jenks 1937, Eason et al. 1967), and Megaselia sp. (Phoridae) (Kaston and Jenks 1937); the neuropteran Mantispa viridis Walker (Mantispidae) (Enders 1974, Tolbert 1976); the coleopteran Chauliognathus sp. (Cantharidae) (Enders 1974); salticid spiders (Salticidae) (Enders 1974); and birds (Enders 1974, Tolbert 1976).

Argiope aurantia prefers vegetation along water courses in Florida (Levi 1968), and is common in roadside hedgerows bordering

drainage ditches. In these habitats, the relative humidity is usually quite high (70-90% RH) in late August-September (the egg-laying and molting period), although exposure to high levels of insolation may cause periodic fluctuations of the RH over a wide range. By late fall, the RH may drop to 30-40%. The temperatures may be buffered somewhat by the vegetation in the summer, but are usually relatively close to ambient, although they may be quite high (35-40° C) in southern exposures. From fall on, the temperatures in the habitat follow ambient air temperature closely.

CHAPTER III
THE "INSULATION" LAYER IN THE COCOONS OF ARGIOPE AURANTIA

Introduction

All spiders place their eggs in some form of silken cocoon (Turnbull 1973). These structures must provide protection for the eggs, create a proper microclimate for embryonic development, hatching, and subsequent molting, and provide a safe retreat for the spiderlings to overwinter until emergence in the spring. Because of the lengthy development and overwintering period of some spiders (Anderson 1978), many cocoons are exposed to severe temperature extremes. Fluctuations in cocoon temperature have been shown to have a direct effect on the development and survival of spider eggs (Norgaard 1956, Schaefer 1976) and spiderlings (Norgaard 1956). Several authors have observed spider behaviors which presumably modify the thermal environment of the cocoon. These include burying the cocoon (Levi and Levi 1969), shuttling the cocoon between different microclimates (Norgaard 1951, Humphreys 1974), and placing it in protected microclimates. Others have suggested that a layer of silk within some cocoons functions as insulation, modifying the thermal environment experienced by the eggs or spiderlings (McCook 1890, Kaston 1948, Turnbull 1973, Gertsch 1979). Schaefer (1976) reported that the cocoons of Floronia bucculenta (Clerck) (Linyphiidae) are capable of protecting the eggs from daily

fluctuations in ambient temperature. However, Austin and Anderson (1978) found no significant differences in the hatching success of spider egg masses, with or without cocoons, exposed to a range of constant temperatures. They concluded that the flocculent silk cocoons of Nephila edulis (Koch) (Araneidae) did not function to protect the eggs from temperature extremes.

The cocoon of Argiope aurantia Lucas (Araneidae) is a multilayered structure, with a flocculent layer of silk located between the eggs or spiderlings and the cocoon cover (see Fig. 2-2b). In late August-September, the cocoons are usually placed in the upper strata of the vegetation where they may be exposed to direct sunlight, wind, and the night sky, all of which may alter the internal temperature of the cocoon throughout the development and overwintering period. Here, I examine the the role of the cocoon, and in particular the effectiveness of the flocculent silk layer within A. aurantia cocoons, in buffering temperature extremes. I also examine the role that cocoon positioning in the habitat plays as an adjunct method of temperature regulation.

Materials and Methods

I used three types of cocoons: whole, nonparasitized cocoons containing spiderlings, and two types of modified cocoons, "insulated" and "non-insulated". The latter two types were created by halving whole cocoons longitudinally with a razor blade and removing either the eggs alone, or the eggs and the flocculent silk layer. The halves of these modified cocoons were rejoined with

clear nail polish. These whole and modified cocoons were mounted on thermal probes (YSI #513, time constant of 0.02 s), with the tip of the probe in the approximate position of the egg or spiderling mass.

Cocoons were allowed to equilibrate to room temperature (T_a = 26° C) in a large cardboard enclosure, and then placed in a styrofoam cooler packed with salted ice. The internal temperature of the cocoon in the cooler was recorded every 30 s until it reached the ambient temperature of the cooler (T_a = 8-9° C). The cooling trials were performed in a dark room to avoid radiant loading from the overhead lights, and with the air conditioning off to minimize the effects of convective cooling from air movement. The walls of the cardboard enclosure and the cooler were monitered with banjo probes (YSI #427, time constant of 1.10 s) taped to the inner surfaces. The temperatures of these surfaces matched the ambient air temperatures within each container. Only data from trials where the ambient temperature in the cooler varied by no more than ± 0.5°C were used for the calculation of the cooling curves.

In the field, the changes in internal temperatures of whole and modified cocoons (using YSI #513 probes) in an artificial closed habitat (1 x 1 x 1 m cardboard enclosure) were recorded at one min intervals for 50 min over an approximate 2.5° C drop in ambient air temperature. On a different day, changes in internal temperatures (YSI #513) of whole and modified cocoons exposed to 10 min radiation loads, and to 2 min loads followed by 8 min of cooling were also recorded. This experiment was conducted between 1100 and 1300 h when the sun was at its zenith. During this time, ambient

temperature was relatively constant (12.9-13.6° C), and there was no wind. All the cocoons used in this experiment were approximately the same size, color, and mass. On a third day, the hourly changes in ambient air temperature (YSI #405 probe, time constant of 0.60 s) and in the internal (YSI #513) and surface temperatures (YSI #427) of two cocoons in two different habitats (closed canopy under trees, open canopy in an old field) were recorded for 24 h. Simultaneous measurements of the sky and vegetation temperatures or enclosure wall temperatures were made with a Stoll-Hardy HL4 radiometer during all of the field experiments to measure the radiant heat load in the respective test habitats.

Results

There were no significant differences between the slopes of the cooling curves for the modified cocoons (Fig. 3-1). Both types of modified cocoons showed cooling rates of approximately 11° C/ min. In contrast, the whole cocoons cooled significantly more slowly than the modified cocoons ($F = 356.71$, $p < 0.001$); the presence of spiderlings (total cocoon weights 0.63 to 0.93 g; spiderling weights 0.56 to 0.83 g) decreasing the cooling rate to approximately 2.0° C/ min (Fig. 3-1).

Outdoors, in the artificial closed habitat, there were no significant differences between the rates of cooling for the whole cocoon (total weight 0.809 g; spiderling weight 0.682 g), and the modified cocoons with and without the flocculent silk layer.

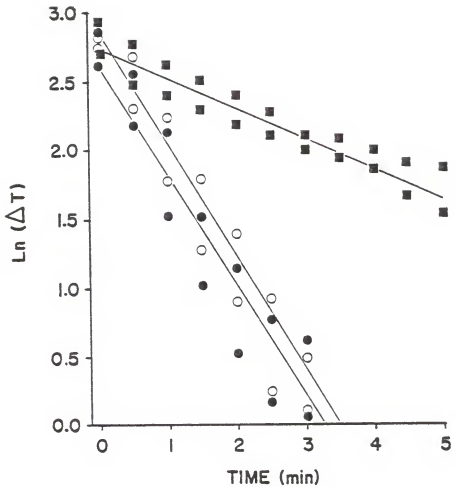


Fig. 3-1. Cooling rates in still air in the laboratory for whole and modified Argiope aurantia cocoons. The whole cocoons (squares) contained spiderlings and the flocculent silk layer; the modified cocoons contained only the flocculent silk layer (open circles), or were empty (closed circles). The cooling curve for the whole cocoons is $Y = -0.208X + 2.73$ ($r^2 = 0.95$, $n = 6$); for the modified cocoons with the flocculent layer $Y = -0.824X + 2.85$ ($r^2 = 0.96$, $n = 10$); for the empty cocoons $Y = -0.810X + 2.66$ ($r^2 = 0.90$, $n = 8$). During cooling $T_a = 8\text{-}9^{\circ}$ C. The data points represent the range for each set of experimental trials.

The internal temperatures of all three cocoons closely followed the change in ambient temperature (Fig. 3-2).

Among the cocoons exposed to radiation loads for 10 min, there was no significant difference between the rates of heating for the modified cocoon with the flocculent silk layer and the cocoon without it (Fig. 3-3). Both cocoons heated rapidly to an equilibrium temperature of 22.5° C in approximately 5 min. The rate of heating for the whole cocoons (total weights 0.9735 g and 0.9025 g; spiderling weights 0.7500 g and 0.7400 g, respectively) was significantly different from that for the modified cocoons ($F = 26.11$, $p < 0.0001$; calculated for the first 4 min). These cocoons heated to approximately 19.0° C in 5 min; an internal temperature some 3.5° C cooler. Beyond this point, they heated at a slower rate. An extension of this second, flatter heating curve suggests that the whole cocoons would not reach the equilibrium temperature of the modified cocoons until another 15 min had elapsed.

The whole and modified cocoons exposed to the 2 min loads heated at the same rates as their counterparts in the 10 min group (Fig. 3-3). The rates for the two groups of cocoons were significantly different from one another as well ($F = 7.490$, $p = 0.034$; calculated on the first 2 min). When the radiation load was removed, the modified cocoons rapidly cooled to ambient air temperature. The whole cocoons also cooled upon removal of the load, but at a much slower rate (Fig. 3-3).

The absolute internal temperature achieved by whole cocoons in the field depended on their location in the habitat. While the

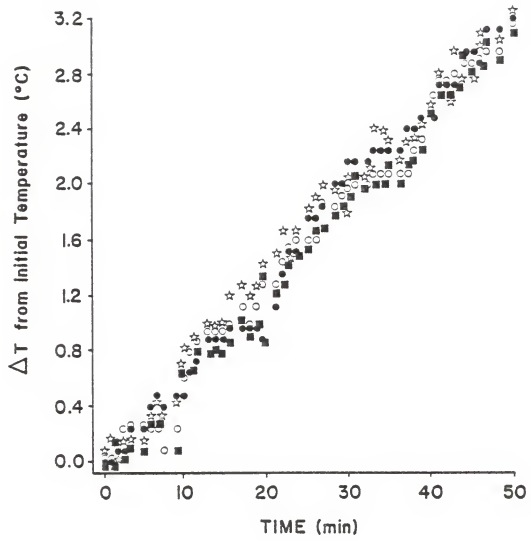


Fig. 3-2. Cooling rates outdoors for whole and modified Argiope aurantia cocoons in an artificial closed habitat (1 x 1 x 1 m cardboard enclosure) over a 50 min period during an approximate 2.5° C change in ambient temperature. The whole cocoon (squares) contained spiderlings and the flocculent silk layer; the modified cocoons contained only the flocculent layer (open circles), or were empty (closed circles). The cooling curve for the whole cocoon is Y = 0.067X - 1.57 (r^2 = 0.99, n = 1); for the modified cocoon with the flocculent layer Y = 0.066X - 1.61 (r^2 = 0.99, n = 1); for the empty cocoon Y = 0.065X - 1.50 (r^2 = 0.98, n = 1). The curve for the change in ambient temperature (stars) is Y = 0.060X - 1.90 (r^2 = 0.99). The temperatures of the top and sides of the enclosure during this period were 4° C and 5° C, respectively.

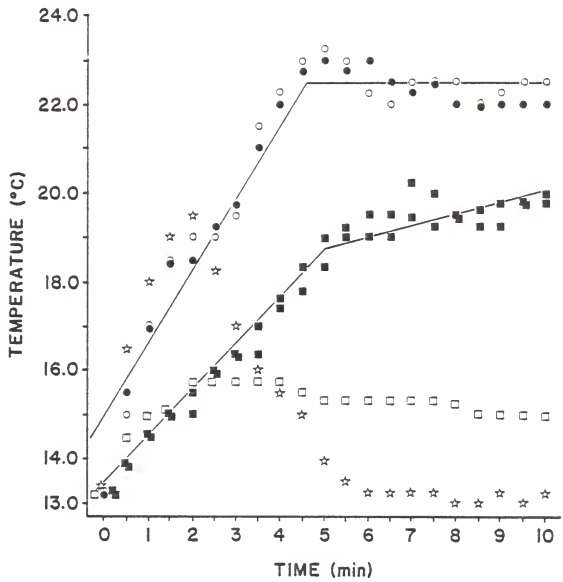


Fig. 3-3. Heating rates in still air outdoors for whole and modified Argiope aurantia cocoons exposed to radiant loads of 2 and 10 min duration. The whole cocoons (open squares, 2 min; closed squares, 10 min) contained spiderlings and the flocculent silk layer; the modified cocoons contained only the flocculent layer (stars, 2 min; open circles, 10 min), or were empty (closed circles, 10 min). The heating curve for the whole cocoons is $Y = 0.50X + 13.44$ ($r^2 = 0.98$, n = 2); for the modified cocoons with the flocculent layer $Y = 1.01X + 14.29$ ($r^2 = 0.93$, n = 1); for the empty cocoons $Y = 0.96X + 14.47$ ($r^2 = 0.94$, n = 1). The ambient air temperature during the experiment ranged from 12.9° C to 13.7° C. The vegetation and sky temperatures during the experiment were +15° C and -20° C, respectively.

cocoon (total weight 0.820 g; spiderling weight 0.724 g) in the sheltered site (under overhanging vegetation) attained highs and lows close to the ambient air temperature, the internal temperature of the cocoon (total weight 0.991 g; spiderling weight 0.842 g) in the exposed site (open field) fluctuated widely, attaining much higher and lower values (Fig. 3-4). The surface temperatures of the cocoons equaled the ambient temperature in the shade ($T_{surf} = T_a$) and were greater than both ambient and the internal temperature of the cocoons in the sun ($T_a < T_{surf} > T_c$).

Discussion

Under laboratory conditions, the internal temperatures of whole and modified A. aurantia cocoons exposed to sudden drops in ambient temperature (from 26° C to 8-9° C) do not change instantaneously (see Fig. 3-1), indicating that some part of the cocoon acts as insulation. However, under these conditions the cooling rates for cocoons with and without the flocculent silk layer are identical, suggesting that it is the cover of the cocoon, and not the flocculent layer, that creates the dead air space that acts as insulation (Kaufman et al. 1982). This explains why Austin and Anderson (1978) found that the coverless, flocculent cocoons of N. edulis offered no protection to their egg masses; these cocoons have little or no dead air space. The whole cocoons also cooled four times more slowly than the modified cocoons (see Fig. 3-1). Presumably, this additional thermal inertia is due to the mass of the spiderlings, which are approximately 70% water (Anderson 1978).

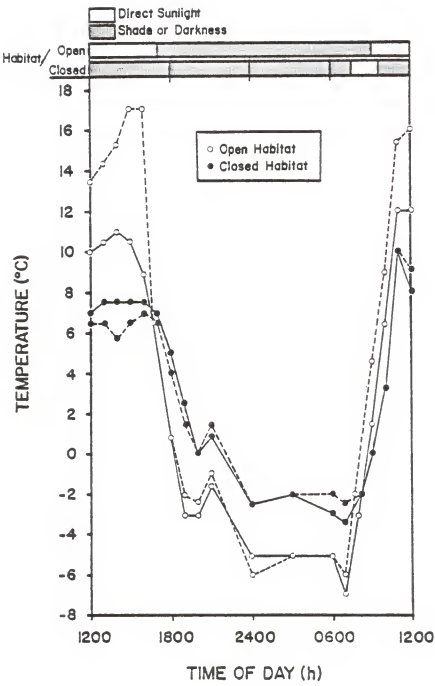


Fig. 3-4. The relationship of internal cocoon temperature to habitat position for two Argiope aurantia cocoons. The solid lines (——) are ambient temperatures, and the dashed lines (---) are internal cocoon temperatures. Over 24 h, the cocoon in the open habitat (old field) was exposed to extended periods of direct sunlight, and faced greater reflected radiation from the vegetation (32° C to -15° C), and colder sky temperatures (2° C to -39° C) than the cocoon in the closed habitat (old field edge under trees) faced from the vegetation (25° C to -10° C), or from the sky (25° C to -17° C).

The cocoon, in combination with the egg or spiderling mass, acts as a buffer against rapid temperature changes (Fig. 3-1). Such rapid changes could result from exposure to the night sky immediately after sundown, particularly in the winter (see Fig. 3-4). However, most A. aurantia cocoons are placed within the vegetation. In these protected locations, radiant heat loss to the cold night sky is reduced by the warmer overhead vegetation. Under these conditions, cooling is slower and follows the change in ambient air temperature (see Fig. 3-2). Cold hardiness (Schaefer 1977, Riddle 1981) resulting from physiological solutions such as freezing point depression (Kirchner and Kestler 1969) probably protects the eggs or spiderlings from extremely cold temperatures.

Cocoons in open habitats but under a layer of vegetation, or in closed habitats such as woods may still be exposed to periodic "sunflecks" as the sun moves across the sky. These short lived, but potentially intense, radiant loads could present a serious thermal challenge to the cocoon. The field experiments indicate that the cocoon and the mass of the eggs or spiderlings provide a significant buffer against short-term loads (see Fig. 3-3), extending the heating time to equilibrium by approximately 15 min. However, the level of protection provided by a cocoon is directly related to the ambient air temperature, the duration of the load, and the elapsed time between consecutive loads. The radiant loading experiments were conducted in the winter, when the ambient air temperature was relatively low (12-14^{o} C). Even with constant exposure to insolation, low ambient temperatures such as these would result in a

low equilibrium temperature (Heath 1964) that is probably below the danger level for the spiderlings in the cocoon. However, during the early part of the reproductive season, when the ambient temperature is relatively high, radiant loads may represent a more serious problem. Under these conditions, a load of long duration could raise the equilibrium temperature of the cocoon past the safe limit for the eggs or spiderlings. Loads of short duration also pose a problem if they occur in rapid enough succession. Under these conditions, the internal temperature of the cocoon would "step" up with each successive load due to the slow rate of heat loss from the egg or spiderling mass (see Fig. 3-3), finally rising above the lethal limit.

Other behaviors may play a role in insuring that the cocoon is not exposed to lethal thermal loads. Argiope aurantia prefers to oviposit beneath a layer of vegetation or among the leaves of broad-leafed plants. Such sites would limit the number and length of insolation bouts the cocoon encounters, particularly during the late summer when oviposition occurs. The comparison of internal temperatures from cocoons in open and closed habitats supports maternal positioning of the cocoon as an important control measure (see Fig. 3-4). Positioning the cocoon in a closed site rather than in an open site resulted in a 10° C difference between the highest internal temperature achieved (because of radiation loading), and a 4° C difference in the lowest temperature achieved (because of exposure to cold night sky temperatures). Although spiderlings can tolerate high temperatures (Tolbert 1979), proper site choice could

mean a few degrees difference in internal cocoon temperature. This difference may be important when the ambient temperature approaches the upper critical temperature of the eggs or spiderlings.

The limited ability of the relatively large A. aurantia cocoons to resist temperature fluctuations suggests that cocoons with smaller masses of eggs or spiderlings will have more difficulty in controlling temperature extremes. The non-functional role of the flocculent silk layer as insulation further suggests that cocoons may function to regulate other factors in the environment. Due to the small size of the eggs and spiderlings, and their consequent high surface area to volume ratio, it seems likely that cocoons may play a role in limiting water loss. This role is explored in Chapter IV.

CHAPTER IV
THE ROLE OF SPIDER EGGS AND COCOONS IN RESISTING WATER LOSS

Introduction

All spiders enclose their eggs in some form of silken cocoon (Turnbull 1973). Within these structures the eggs undergo embryonic development, hatch to the deutova stage, and molt to the spiderling stage. The spiderlings then spend from 6 to 10 months in the cocoons until emergence in the spring. Dessication may be a problem for these developmental stages. Many insects use cocoon-like structures to limit dessication (Chapman 1967, Chauvin et al. 1979), and this is commonly assumed to be the function of cocoons as well (Bristowe 1941, pg. 421; Foelix 1982, pg. 200). Few data exist, however, to support this view. Schaefer (1976) showed that the parchmentlike cocoon of Floronia bucculenta (Clerck) (Linyphiidae) increased the survival time of post-diapause eggs exposed to a RH of 32% (at 5° C) from 37 to 68 days. Austin (1984) has demonstrated that the silk nests containing eggs of Clubiona robusta L. Koch (Clubionidae) increases humidity levels. The casual observations of McEwon (1963) also suggest that the flocculent cocoon of an Australian Nephila sp. (Araneidae) provides desiccation protection for the spiderlings. Austin and Anderson (1978), however, have showed that the flocculent silk cocoon of the congener N. edulis

(Koch) has no effect on the hatching success of spider egg masses at different controlled humidities.

Some spider eggs are dessication-resistant as well (Schaefer 1976). This resistance may result from a layer of spherical granules on the chorion surface (Austin and Anderson 1978, Grim and Slobodchikoff 1978, 1982, Humphreys 1983). Overwintering spiderlings within the cocoon can also attenuate water loss by reducing their rates of metabolism (Schaefer 1976, Anderson 1978), or by metabolizing lipids. Presumably, the cuticle of spiderlings also impedes water loss (Lees 1947, Davies and Edney 1952).

I investigate here the role of the cocoon in controlling water loss from the egg and spiderling masses of Mecynogea lemniscata (Walckenaer) and Argiope aurantia Lucas (Araneidae) during egg development, deutoval molting, and spiderling overwintering. I also examine the effect of clutch size, and egg morphology (Austin and Anderson 1978, Grim and Slobodchikoff 1978, 1982) on water loss.

Materials and Methods

The Cocoons and Their Habitats

The cocoons of M. lemniscata and A. aurantia differ in size, density of the cover, and internal construction. The preferred habitats of the two spiders also differ, the habitat of M. lemniscata being more consistently humid than that of A. aurantia (see Chapter II).

Experimental Material

The cocoons and egg masses of A. aurantia were obtained from spiders collected in the field and maintained at 24-25°C and 60-70% RH in 500 ml jars in the laboratory. The M. lemniscata cocoons and egg masses were obtained by daily censusing 100-150 marked web-sites. The cocoons used in the experiments on spiderling survival were collected in the field in late August (for M. lemniscata), and during September-October (for A. aurantia). Only undamaged, nonparasitized cocoons were utilized. The experimental spiderling masses were obtained by removing the cocoon cover and as much of the internal flocculent layer of silk as possible.

Egg Surface Morphology

The surfaces of M. lemniscata and A. aurantia eggs were photographed with a Hitachi S-415A SEM. They were prepared by attaching them to SEM stubs with double-sided tape, and coating with 75 Å of gold. The densities of the spherical granules (spheres) on egg surfaces were measured by placing a grid system (4 x 4 lines) over the electronmicrographs of five eggs of each species and counting all spheres within 2 randomly chosen grid-squares. Since the spheres on both species' eggs are distributed essentially as monolayers (Humphreys 1983), densities were expressed as the mean number of spheres/ 100 μm^2. Sphere diameters were determined directly by measuring all the spheres within the 10 grid-squares.

Effect on Dessication

The effects of the sphere layer, clutch size, and the cocoon on hatching success, molting success, and spiderling survival were determined by rearing intact egg and spiderling masses without cocoons (and appropriate controls) at 25-26° C in one liter jars controlled at four different RH levels (0%, 33%, 66%, and 100%). The controlled humidities were achieved by using dry anhydrous KOH pellets (0% RH), and saturated salt solutions of 300+ g $CaCl_2$/ 100ml H_2O (33% RH), 100 g $NaNO_2$/ 100 ml H_2O (66% RH), and 15 g K_2SO_4/ 100 ml H_2O (100% RH) (Winston and Bates 1960, Peterson 1964). The pellets and solutions controlling the humidities were changed every two weeks. Since the egg masses of A. aurantia contain more eggs than those of M. lemniscata (approximately 970 to 20, respectively), artificially reduced egg masses of 15-25 A. aurantia eggs were also reared under these conditions to control for the possible effects of egg mass size on hatching success.

The effect of the cocoon was also tested under field conditions by placing intact egg and spiderling masses (and appropriate controls) in individual screen-covered vials within styrofoam-cup housings. These housings protected the replicates from precipitation, predators, and parasites, and were hung in the shade in locations where females had previously constructed cocoons.

Hatching and molting success was calculated after 30 days. Hatching success was the percentage of total eggs in which the chorion ruptured and a deutova successfully emerged. Molting

success was the number of these deutova which successfully molted to the first instar spiderling stage. Spiderling survival was determined using separate masses, and was calculated after the experiments had run for 90 days.

Results

The Sphere Layers

The spheres associated with the eggs of M. lemniscata and A. aurantia are shown in Fig. 4-1. For both, the sphere diameter ranged from 0.40 to 7.20 μm. The mean diameter in M. lemniscata eggs was not significantly different from that of A. aurantia eggs (Table 4-1). However, the mean sphere density (spheres/ 100 μm^2) of M. lemniscata eggs was significantly greater ($t = 2.11$, $df = 20$, $p < 0.05$) than that of A. aurantia eggs.

The Effect of Clutch Size and the Sphere Layer

No significant differences in hatching success at 100% RH were found between intact and reduced A. aurantia egg masses without cocoons at each humidity (Table 4-2). Reduction of the egg mass, however, did have a significant effect at 66%, 33%, and 0% RH, indicating that the size of the egg mass of this spider is important to dessication control. There were no significant differences at 100%, 66%, and 33% RH when the hatching success of intact M. lemniscata and A. aurantia egg masses without cocoons was

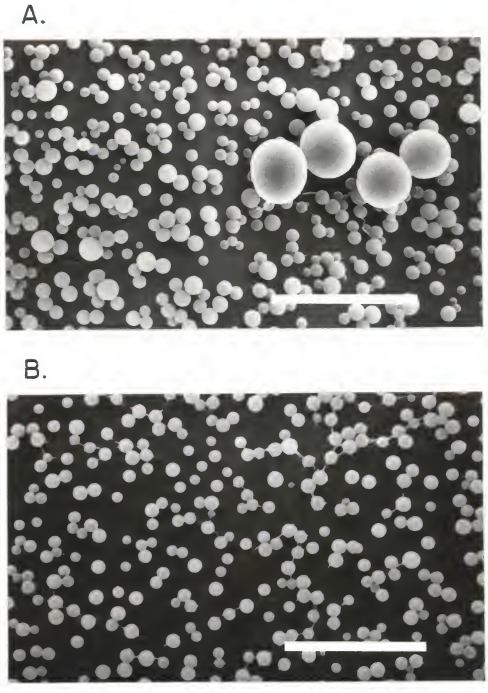


Fig. 4-1. The layer of spherical mucoid granules on the chorionic surface of a Mecynogea lemniscata egg (A), and an Argiope aurantia egg (B). The scale line in each case equals 15 μm. Both eggs were plated with 75 Å of gold and observed using secondary electrons.

Table 4-1. The distributions of sphere sizes found on the chorionic surfaces of Mecynogea lemniscata and Argiope aurantia eggs. The mean sphere sizes and mean sphere densities (± 1 SD; n in parentheses) are given below the frequency column for each species.

Sphere Size Diam. (μm)	Frequency	
	M. lemniscata	A. aurantia
0.40 - 0.79	9	2
0.80 - 1.19	57	17
1.20 - 1.59	104	117
1.60 - 1.99	47	26
2.00 - 2.39	12	2
2.40 - 2.79	3	0
2.80 - 3.19	1	0
3.20 - 3.59	2	0
3.60 - 3.99	0	0
4.00 - 4.39	2	0
4.40 - 4.79	0	1
4.80 - 5.19	1	2
5.20 - 5.59	1	0
5.60 - 5.99	1	0
6.00 - 6.39	1	0
6.40 - 6.79	0	0
6.80 - 7.19	1	1
Mean Sphere Size	$\bar{X}$ = 1.56 ± 0.79 (242)	$\bar{X}$ = 1.52 ± 0.70 (168)
Mean Sphere Density	$\bar{X}$ = 21.60 ± 5.46 (10)	$\bar{X}$ = 17.00 ± 4.22 (10)

Table 4-2. Mean percentages of eggs successfully hatched (± 1 SD; n in parentheses) at the four experimental humidities for intact Mecynogea lemniscata and Argiope aurantia egg masses with and without cocoons, and for reduced A. aurantia egg masses without cocoons. Pair-wise comparisons between treatments are by Mann-Whitney U Tests; pair-wise comparisons between humidities within treatments are by nonparametric multiple comparison tests (Zar 1984).

	% Hatching Success				
	M. lemniscata		A. aurantia		
Relative Humidity	Cocoon	No Cocoon/ Intact	No Cocoon/ Reduced	No Cocoon/ Intact	Cocoon
100%	94.9 ± 13.5% (10)	98.3 ± 3.1% (8)	96.2 ± 4.0% (5)	99.7 ± 0.5% (8)	100% (8)
			**	*	
66%	95.4 ± 14.6% (10)	97.4 ± 4.6% (10) ***	49.2 ± 36.8% (8) **	94.3 ± 11.3% (8)	90.0 ± 24.8% (7)
				*	
33%	96.9 ± 7.9% (10)	88.7 ± 15.5% (10) ***	28.7 ± 32.3% (10) **	87.9 ± 7.0% (9) **	96.6 ± 5.8% (7)
	***	***			
0%	3.4 ± 7.3% (10)	3.6 ± 8.3% (10)	6.7 ± 5.7% (10) ***	70.4 ± 22.8% (8) *	88.2 ± 17.5% (8)
Kruskall-Wallis H	29.43	25.80	17.70	21.70	8.29
"P"	< 0.001	< 0.001	< 0.001	< 0.001	< 0.05

(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

compared at each humidity. There was a significant difference at 0% RH, underscoring the advantage of a large egg mass.

A different pattern of hatching success was revealed when intact M. lemniscata egg masses without cocoons were compared to reduced A. aurantia egg masses without cocoons at each humidity (Table 4-2). The significant advantage previously demonstrated by the whole A. aurantia egg masses at 0% RH disappeared, and hatching success dropped significantly below that of M. lemniscata at 66% and 33% RH, presumably because of differences in the densities of the the sphere layers covering the eggs of each species. There were no significant differences at 100% RH, where dessication is obviously not a problem.

The Effects of the Cocoons

Cocoon removal had no effect on the hatching success of M. lemniscata at any experimental humidity (Table 4-2). Below 33% RH, there were significant decreases in hatching success for egg masses with and without cocoons. Molting success showed no significant reduction with cocoon removal at any experimental humidity (Table 4-3). Since few eggs hatched at 0% RH, however, the percentage of total eggs which ultimately molted was small. The cocoon did have a significant effect on spiderling survival. At all the experimental humidities survival was greater with a cocoon (Table 4-3). The field results support these findings (Table 4-4); only spiderling survival was significantly affected by removal of the cocoon.

Table 4-3. Mean percentages for molting success and spiderling survival (± 1 SD; n in parentheses) at the four experimental humidities for Mecynogea lemniscata egg and spiderling masses with and without cocoons. Pair-wise comparisons between treatments are by Mann-Whitney U Tests; pair-wise comparisons between humidities within treatments are by multiple range tests (Zar 1984).

Relative Humidity	% Molting Success		% Spiderling Survival		
	Cocoon	No Cocoon	Cocoon		No Cocoon
100%	100% (8)	99.1 ± 2.5% (8)	100% (13)	***	80.0 ± 25.1% (6)
			**		
66%	100% (10)	100% (10)	81.9 ± 29.8% (13)	**	56.2 ± 28.8% (14)
			*		***
33%	100% (10)	100% (10)	47.4 ± 38.1% (11)	***	1.0 ± 2.7% (14)
			**		
0%	100% (10)	100% (10)	6.8 ± 13.7% (14)	**	0% (14)
Kruskall-Wallis H	0.00	0.00	35.44		38.22
"p"	1.00	1.00	< 0.001		< 0.001

(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Table 4-4. Mean pecentages (± 1 SD; n in parentheses) for hatching and molting success and spiderling survival in the field for the spiders Mecynogea lemniscata (ML) and Argiope aurantia (AA). Conditions in the field (60-80% RH and 24-32°C) approximated the laboratory conditions at 66% RH. The data are presented as percentages, but were arc-sine transformed for the statistical analyses (Sokal and Rohlf 1969).

	% Hatching Success		% Molting Success		% Spiderling Survival	
Spider	Cocoon	No Cocoon	Cocoon	No Cocoon	Cocoon	No Cocoon
ML	99.6 ± 1.9% (19)	99.3 ± 2.7% (17)	100% (19)	100% (17)	98.2 ± 12.7% (21)	50.7 ± 27.0% (10)
					***	
	Cocoon	No Cocoon	Cocoon	No Cocoon	Cocoon	No Cocoon
AA	99.8 ± 0.7% (10)	99.8 ± 0.4% (10)	100% (10)	100% (10)	93.3 ± 0.9% (10)	91.8 ± 2.9% (10)

*** F-test: F = 15.12, df = 29, p = 0.005.

The results for A. aurantia differed from those for M. lemniscata. In the laboratory, cocoon removal had no significant effect on hatching success at 100%, 66%, or 0% RH, although it did significantly affect success at 33% RH (Table 4-2). Cocoon removal had no significant effect on molting success at any experimental humidity. However, at 33% and 0% RH the variances in the non-cocoon cells were much larger, suggesting that an effect may have been difficult to detect. Molting success fell off significantly below 66% RH with and without a cocoon (Table 4-5). The absence of a cocoon also made no difference in spiderling survival at either 100% RH or 66% RH (Table 4-5). However, below 100% RH spiderling survival significantly declined with and without cocoons, and below 66% RH all the spiderlings died after 90 days regardless of the treatment. The results from the field experiments support the laboratory results at 100% and 66% RH (Table 4-4). Under field conditions, cocoon removal had no significant effect on egg hatching success, molting success, or spiderling survival.

Discussion

The results indicate that the enclosed cocoons of M. lemniscata and A. aurantia do not affect water loss from the egg stage. These findings are paradoxical, since they support the findings of Austin and Anderson (1978) for a flocculent cocoon, but do not agree with Schaefer's (1976) findings for a covered cocoon. This paradox may be explained by the amount of time the eggs of these spiders spend in the cocoon. The developmental times of M. lemniscata

Table 4-5. Mean percentages for Molting Success and Spiderling Survival (± 1 SD; n in parentheses) at the four experimental humidities for Argiope aurantia egg and spiderling masses with and without cocoons. Pair-wise comparisons between treatments are by Mann-Whitney U tests; pair-wise comparisons between humidities within treatments are by nonparametric multiple comparson tests (Zar 1984).

	% Molting Success		% Spiderling Survival	
Relative Humidity	Cocoon	No Cocoon	Cocoon	No Cocoon
100%	100% (8)	100% (8)	98.8 ± 1.5% (7)	93.7 ± 8.2% (5)
			**	**
66%	100% (7)	99.1 ± 2.0% (8)	61.5 ± 27.5% (6)	63.5 ± 19.6% (8)
	***	**	***	***
33%	96.0 ± 4.2% (7)	76.2 ± 34.8% (9)	0% (8)	0% (8)
0%	84.4 ± 19.0% (8)	56.1 ± 48.0% (8)	0% (9)	0% (9)
Kruskall-Wallis H	22.40	11.09	27.18	27.99
"p"	< 0.001	< 0.01	< 0.001	< 0.001

(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

and A. aurantia are relatively short (15-20 days and 20-30 days, respectively), and even at low humidities this may not be long enough to demonstrate the water retaining qualities of the cocoon. In contrast, the eggs of F. bucculenta remain within the cocoon in winter diapause for approximately 180 days. Since the eggs are not particularly drought resistant (Schaefer 1976), they probably lose water during this time. The significant effect of the cocoon on egg survival, that Schaefer demonstrated, can probably be attributed to his use of post-diapause eggs, from which enough water had already been lost to make the effect of cocoon removal apparent.

The significant difference in hatching success between intact and reduced A. aurantia egg masses without cocoons demonstrates that clutch size can affect hatching success as well. Spider egg masses are usually agglutinated, and as the mass gets larger, its surface area to volume ratio declines as a greater number of eggs are positioned completely within the mass. Presumably, this difference also accounts for the difference in hatching success between intact M. lemniscata and A. aurantia egg masses without cocoons at 0% RH (see Table 4-2).

The ability of intact M. lemniscata egg masses without cocoons to maintain hatching success rates equal to those of the much larger A. aurantia egg masses at humidities above 0% RH indicates that some factor other than clutch size is also operating to control water loss (see Table 4-2). A number of authors have suggested that a layer of spherical mucoid granules (Austin and Anderson 1978) on the chorions of spider eggs functions to control water loss by reducing

the free surface area through which water can pass (Austin and Anderson 1978, Grim and Slobodchikoff 1978, 1982, Humphreys 1983). The eggs of M. lemniscata have a significantly denser coating of these spheres than do the eggs of A. aurantia (see Table 4-1). Although a direct comparison of the eggs of each of these species with and without spheres is difficult (due to problems in stripping the sphere layer from the eggs and still maintaining viability), the comparison of intact M. lemniscata egg masses with reduced A. aurantia egg masses strongly suggests that the sphere layer does reduce water loss (Table 4-2). However, the drop in hatching success at 0% RH indicates that this barrier has limits in its ability to control water loss at very low humidities.

Molting is a dangerous period of time for deutova with their high surface area to volume ratio (Horner and Starks 1972). At molting, with the breaking and subsequent shedding of the egg chorion, dessication protection shifts back to the level of the cocoon. In spite of this, removal of the cocoons of M. lemniscata and A. aurantia demonstrate no effect on molting success (see Tables 4-3 and 4-5). However, the variances among the no-cocoon treatments of A. aurantia at 33% and 0% RH are high, which may make detection of the cocoon's effect on molting success difficult. Presumably, the main factor affecting molting success for these spiders is the ambient RH at the oviposition site, although the greater molting success of M. lemniscata at low humidities suggests that there may be morphological or physiological differences in the abilities of the deutova of these species to reduce water loss.

The cocoon of A. aurantia also appears to have little effect on spiderling survival. The lack of a cocoon effect on hatching and molting success, and the significant drops in molting success and spiderling survival below 66% RH suggest that other considerations are more important to reducing desiccation. Field observations of damaged A. aurantia cocoons suggest that the large clutch size of this species may protect the eggs from dessication [which may also explain McEwon's (1963) observation for the Nephila sp.]. However, the RH within the habitat or microhabitat used for oviposition is probably most critical for A. aurantia. Indeed, Levi (1968) notes that of the Argiope species in Florida, A. aurantia prefers moist habitats such as pond edges and stream borders, and is one of the first Argiope species to disappear during drought years.

Removal of the cocoon does have a significant effect on the spiderling survival of M. lemniscata at all experimental humidities (see Table 4-1), and in the field under ambient conditions (see Table 4-3). This spider is the first of the orb-weavers to become active in the spring, emerging in late March. Growth is rapid. Reproduction begins by late June and the adults die by early to mid-August. This early emergence and rapid disappearance is apparently a means of taking advantage of the abundant prey in the habitat, while avoiding competition with other orb-weavers whose populations increase rapidly by August (Anderson 1978). The spiderlings then spend approximately 290 days in the cocoon until they emerge the following March; 2 to 3 months longer than most other orb-weavers (Anderson 1978). The cocoon is apparently part of

a suite of adaptations for controlling water loss [including depressed metabolic rates (Schaefer 1976, Anderson 1978), and lipid-rich eggs (Anderson 1978)], and fits into the foraging/reproductive strategy of this spider by providing a desiccation-resistant refuge in which the spiderlings spend these additional months overwintering.

A number of the egg and spiderling replicates of M. lemniscata and A. aurantia held at 100% RH in the laboratory were attacked and destroyed by fungus. Although these replicates were removed prior to data analysis, in some cases there was still a significant reduction in survival without cocoons at 100% RH (see Table 4-3 for M. lemniscata spiderlings), a humidity where survival should be unaffected by desiccation. This suggests that the covers of cocoons may be related to resisting fungal attack (Christenson and Wenzl 1980), possibly by limiting the amount of water which can enter the cocoon. Chapter V addresses this possibility, and considers the cocoon as a barrier to fungal attack.

CHAPTER V
THE ROLE OF THE COCOON IN LIMITING EXCESS WATER
AND FUNGAL ATTACK

Introduction

Although desiccation is a problem for developing spider eggs and overwintering spiders, too much water may also cause adverse effects. Water, entering the cocoon, could dissolve materials from the egg surface and lower the resistance of the eggs to disease (Austin and Anderson 1978). It could also drown the contents of the cocoon (Schaefer 1976, Reichert 1981). Water may also introduce fungal spores that are pathogenic to the eggs or spiderlings. Christenson and Wenzl (1980) suggested that the cocoon of Nephila clavipes (Linneaus) (Araneidae) protects against fungal attack by reducing the chance of spores gaining access to the egg mass. A role in protecting the eggs and spiderlings from fungi seems reasonable, since both spiders (Bijl and Paul 1922, Nellist 1965) and their eggs (Seligy 1971, Christenson and Wenzl 1980) are attacked by fungus.

Both Mecynogea lemniscata and Argiope aurantia utilize a covered cocoon (see Figs. 2-1 and 2-2), in contrast to the flocculent silk type used by many other orb-weavers (McCook 1890, Scheffer 1905, Kaston 1948). Both spiders also utilize habitats where high humidity during the egg laying period may promote fungal attack (see Chapter II). In this chapter, I examine the roles of

the suspension systems, the internal flocculent layers, and the coverings of the cocoons of these spiders in protecting the eggs and spiderlings from excess water, drowning, and fungal attack.

Materials and Methods

Laboratory Experiments

The abilities of the cocoon suspension system, the cocoon cover, and the internal flocculent silk layer to limit the access of water to, or into the cocoon were examined in the laboratory using M. lemniscata or A. aurantia cocoons as appropriate. The temperature and humidity in the laboratory during all the experiments were 25° C and 50-60% RH, respectively.

To examine the function of cocoon suspension systems in shedding water, M. lemniscata cocoon strings were hung between two vertical supports by their silk suspension lines (see Fig. 2-1). The angle of inclination of the suspension lines was set at 10, 20, 30, and 45° from the horizontal. At each of these angles, water was applied to the suspension lines with a dropper, and its course down the lines noted.

The ability of cocoons to shed water was examined by applying 1.00 ml of water with a syringe directly to hanging strings of M. lemniscata cocoons. The runoff was collected, and the amount retained by the cocoon string calculated. Both naked strings, and those covered with a layer of silk and detritus (see Fig. 2-1c) were tested in this manner. The abilities of both M. lemniscata and

A. aurantia cocoons to shed water were also examined in the field during periods of rain.

To determine whether water actually penetrates the cocoon cover, 10 samples of 2-3 dry M. lemniscata cocoons were submerged in distilled water for time periods of 7, 15, 30, 60, 120, 240, and 480 min. Upon removal from the water, they were blotted on Whatman #1 filter-paper discs for 1 min to remove surface water, and weighed on a Mettler AK 160 balance to the nearest 0.0001 gm. The 10 samples were air dried for 24 hrs between each submersion. After the last submersion bout (480 min), the 22 cocoons comprising the 10 samples were opened and examined under a microscope for the presence of water.

The volume of water absorbed by each cocoon sample was calculated from the increased weight of the sample (1 gm water = 1 ml = 1 cc). This was normalized to ml/ cm^2 by dividing the volume of water by the combined surface area of the cocoons in each sample. A mean value was then calculated from the 10 values for each submersion time.

The role of the flocculent silk layer in resisting water was also tested. Here, flocculent silk from A. aurantia cocoons was used. Uncompressed pieces of this layer were placed on glass slides and drops of distilled water were applied to the silk. The pieces were observed for approximately 10 min, and any wetting of the silk through wicking was noted.

Field Experiments

The function of the cocoon suspension system and the cocoon cover in limiting fungal attack and drowning were investigated by modifying these components in the field, and assessing their effect on egg hatching success and spiderling survival. The cocoons used in these studies were either reared in the laboratory, or collected in the field from marked web-sites. Only nonparasitized cocoons were used.

The cocoons were assigned to the four experimental groups listed below. The experiments using cocoons with eggs were run for 30 days; those using cocoons with spiderlings for 90 days. The cocoons not associated with apparatus were marked by plastic flagging attached to the vegetation.

Vegetation contact. The effect of cocoon suspension systems in preventing fungal attack was examined by placing M. lemniscata cocoons in contact with the vegetation. This simulated partial collapse of the suspension system, and placed limitations on the cocoons drying normally. Placement was accomplished by cutting the cocoon free, and tying it in place to the vegetation with its support line. Access to the cocoons by terrestrial predators was controlled by applying tack-trap to the branches below the cocoons, and pruning the branches above the cocoon so they did not contact the surrounding vegetation. Argiope aurantia cocoons were not subjected to this treatment.

Ground placement. This manipulation also tested the function of the suspension system, but placed the cocoons in a wetter microhabitat where drying was more difficult and the chance of fungal attack or drowning was greater. Both M. lemniscata and A. aurantia cocoons were placed on the ground in enclosures. For A. aurantia cocoons, these were constructed of hardware cloth (1/4" mesh), and were 10 x 10 x 10 cm in size. The enclosure for M. lemniscata cocoons was similar in design, but was constructed of aluminum window screen, and was 5 x 5 x 5 cm in size. These enclosures allowed exposure of the cocoon to the elements, protected them from large predators (although ants could still get in), and prevented them from washing away during heavy rain storms. They were placed below positions where cocoons had previously been collected.

Cover removal. To determine the roles that the covers of M. lemniscata and A. aurantia cocoons play in controlling fungal attack, approximately 20-30% of their covers were removed. During the cover modification, care was taken not to disturb the flocculent silk layer (see Fig. 2-2b), or damage the eggs or spiderlings. The cocoons of M. lemniscata were modified in place in their respective strings. They were treated normally by the female spiders, which remained at the web-site after the modification. The laboratory produced cocoons of A. aurantia were modified, and attached by alligator clips to the arms of a support system. The support was placed in the vegetation in areas where cocoons where already

hanging. Tack-trap was applied to the support arms to limit the access of terrestrial predators (primarily ants).

Cover removal control. This group functioned as a control for possible contaminating effects of the alligator clips. The clips were attached to the necks of cocoons hanging normally in the habitat, and the cocoons were observed for any detrimental effects.

Control. A number of cocoons were subjected to no structural intervention, and functioned as a control for the handling effects in the vegetation placement, ground placement, and cover removal experiments.

Results

Laboratory Experiments

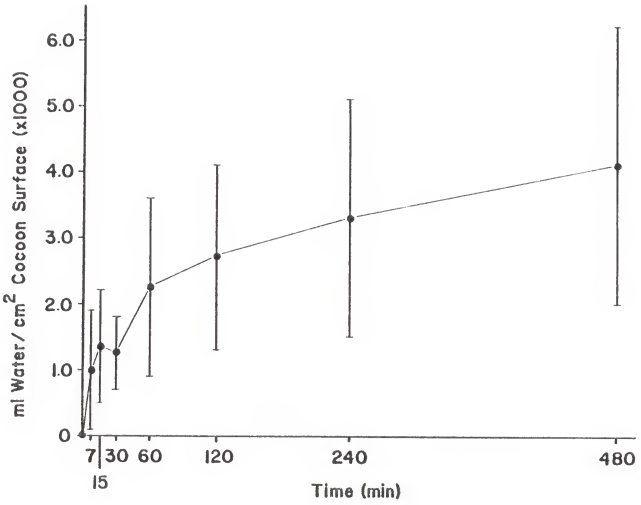
The suspension lines of M. lemniscata cocoons are relatively poor conductors of water. At all the inclinations tested, dry lines were not easily wetted, and consequently tended to shed water. Suspension lines could be wetted by rubbing them between wet fingers, but even here water moved with difficulty. At the lower angles of inclination (10 and 20°), water applied to the wetted line formed drops or beads and hung in place. At the higher inclinations (30 and 45°), water moved down the line toward the cocoons. However, the suspension lines of M. lemniscata cocoons are made of multiple strands of silk and contain "knots" and incorporated debris. When water moving down the line got to these points it built to a drop and fell from the line.

The cocoons of M. lemniscata also shed water well. Depending on whether the cocoon string is naked, or covered with a layer of old web and detritus (see Fig. 2-1), approximately 0.85 to 0.95 ml of the 1.00 ml of water applied to the cocoon string with a syringe was shed immediately. Most of the remaining water forms a droplet at the end of the last cocoon in the string, or remains in the silk over-layer where it disappears by evaporation. Observations of M. lemniscata and A. aurantia cocoons under rainy conditions in the field yielded results similar to those observed in the laboratory. The suspension lines of both species had beads of water hanging on them and appeared not to conduct water toward the cocoons. Both cocoons also shed drops of water from the bottom of the cocoon or end of the cocoon string.

The ability of cocoons with covers to rapidly shed water appears to be related to the slow rate at which their covers absorb water (Fig. 5-1). Over a 2-hr period, the covers of averaged sized M. lemniscata cocoons (0.5 cm^2 in total surface area), absorb only 0.0014 ml of water. Even after 8 hrs of immersion, the amount of water absorbed has increased to only 0.0020 ml.

The thickness of the covers of M. lemniscata cocoons vary between 0.3 and 0.8 mm. The cover is not solid, rather it is a matrix of fibers with included air spaces, similar to fiberglass insulation. Assuming that approximately 50% of the cover is airspace that can be replaced with water, the cover should be able to hold between 0.0015 and 0.0039 ml of water. The 0.0020 ml of water absorbed by the cocoon after 8 hrs of immersion is consistent

Fig. 5-1. The rate of water loading in the laboratory for the covers of Mecynogea lemniscata cocoons submerged in distilled water. The dots represent the mean volume of water absorbed per unit area; the bars represent the SD; n, the sample size, equals 10.


ml Water / cm^2 Cocoon Surface (x1000)
6.0
5.0
4.0
3.0
2.0
1.0
0
7
15
30
60
120
240
480
Time (min)

with these calculations, and suggests that it is the cover alone which absorbs water before the excess is shed by the cocoon. Examination of the cocoons under the microscope supports this. None of the 22 cocoons had water inside them after 4 hrs of submersion.

The flocculent layer of A. aurantia cocoons was completely non-wettable. Water applied to the silk simply formed beads and sat upon the silk until it disappeared by evaporation.

Field Experiments

The incidence of fungal attack on M. lemniscata cocoons containing eggs in the control group was 7.3% (Table 5-1). Chi-square tests between this group, and the Vegetation Contact, Ground Placement, and Cover Removal groups revealed no significant differences in the number of cocoons in the egg stage attacked by fungus. This suggests that neither the cocoon cover, nor the cocoon suspension system function to protect the eggs from fungal attack. There was, however, a significant increase in egg mortality among those cocoons placed on the ground ($X^2 = 12.39$, df = 1, $p < 0.005$). The eggs in these cocoons were all killed, presumably by drowning. They were not covered with fungus.

The natural incidence of fungal attack on M. lemniscata cocoons in the spiderling stage was 1.0% (Table 5-2). Contact with the vegetation did not significantly increase the number of cocoons attacked by fungus in this stage. However, there were significant increases in the number of cocoons attacked by fungus among those placed on the ground ($X^2 = 9.93$, df = 1, $p < 0.005$). Cocoons with

Table 5-1. The effect of modification of the cocoon suspension system and cover on the incidence of fungal attack on the eggs of Mecynogea lemniscata. Cocoons in the "Other" category contained eggs which were not attacked by fungi, but did not hatch due to inviability or drowning. In many cases the eggs rotted. All cocoons were collected after 30 days.

Experimental Modification	Sample Size	Successful Hatching	Fungal Attack	% Cocoons Attacked	Other
Control	171	153	12	7.3%	6
Vegetative Contact	21	18	3	14.3%	0
Ground Placement	19	12	2	14.3%	5
Cover Removal	13	12	1	7.7%	0

Table 5-2. The effect of modification of the cocoon suspension system and cover on the incidence of fungal attack on the spiderlings of Mecynogea lemniscata. Cocoons in the "Other" category contained spiderlings which were not attacked by fungi, but did not survive due to drowning. All cocoons were collected after 90 days, except for those placed on the ground. They were collected after 45 and 90 days.

Experimental Modification	Sample Size	Successful Survival	Fungal Attack	% Cocoons Attacked	Other
Control	239	236	3	1.7%	0
Vegetation Contact	65	63	2	3.2%	0
Ground Placement (45)	22	17	3	17.6%	2
(90)	12[a]	11	1	11.0%	0
Cover Removal	37	32	5	15.6%	0

[a] A number of cocoons were attacked by ants in this group and could not be used for the analysis. This explains the low percentage of fungal attack after the longer 90-day period.

modified covers also had significantly higher rates of fungal attack ($\chi^2 = 13.03$, df = 1, $p < 0.005$). In addition, spiderling mortality due to other causes, probably submersion and subsequent drowning, was significantly higher on the ground ($\chi^2 = 13.34$, df = 1, $p < 0.005$).

The incidence of fungal attack on the cocoons of A. aurantia was very low in both the egg stage (4.9%; Table 5-3), and the spiderling stage (0%; Table 5-4). Chi-square tests between the Control group, and the Ground Placement and Cover Removal groups revealed no significant differences in the number of cocoons attacked by fungus in either the egg stage or the spiderling stage. The two Control groups were not significantly different from each other.

Discussion

The suspension systems of both M. lemniscata and A. aurantia cocoons are difficult to wet, and conduct water poorly. Consequently, they act to discourage water from moving down the lines to the cocoons. The covers of both cocoons shed water effectively, and apparently absorb only a small amount. Presumably, the flocculent silk layers of both cocoons are also difficult to wet, and function further to limit the water from entering the cocoon. All of these structures ultimately function to keep the cocoon dry by channeling water away from it. However, the connection between this function, and the prevention of fungal attack is not clear. Modification of the cocoon cover and partial

Table 5-3. The effect of modification of the cocoon suspension system and cover on the incidence of fungal attack on the eggs of Argiope aurantia. Cocoon modification had no effect on egg inviability or drowning. All cocoons were collected after 30 days.

Experimental Modification	Sample Size	Successful Hatch	Fungal Attack	% Cocoons Attacked
Control	41	39	2	4.9%
Ground Placement	12	10	2	20.0%
Cover Removal	13	11	2	15.4%

Table 5-4. The effect of modification of the cocoon suspension system and cover on the incidence of fungal attack on the spiderlings of Argiope aurantia. No spiderlings were killed by drowning in these experiments. All cocoons were collected after 90 days.

Experimental Modification	Sample Size	Successful Survival	Fungal Attack	% Cocoons Attacked
Control	40	40	0	---
Ground Placement	22	22[a]	0	---
Cover Removal	20	20	0	---

[a] Of the 22 cocoons, 2 had small patches of fungus on the shell, but the contents were unaffected.

collapse of the suspension system of M. lemniscata cocoons is unrelated to the incidence of fungal attack in the egg stage (see Table 5-1). Even total failure of the suspension system did not result in increased fungal attack, although cocoons placed on the ground did suffer higher egg mortality due to drowning.

The integrity of the suspension system and cocoon cover was important to M. lemniscata cocoons that contained spiderlings (see Table 5-2). In this stage, total collapse of the suspension system resulted in increased mortality due to drowning. The incidence of fungal attack also increased with modification of the cocoon cover. However, it is unclear whether the spiderlings were attacked by fungus because of damage to the cover, or died for some other reason and were subsequently attacked. Modifying the cocoon cover does increase dessication problems for M. lemniscata spiderlings (see Chapter IV), and this may have been the real cause of the increased spiderling death. However, I have also had fungus attack spiderlings in the laboratory under conditions of high relative humidity (66-100% RH) where dessication should not be a problem.

Christenson and Wenzl (1980) found that 17.5% of the cocoons of N. clavipes were attacked in the egg stage by fungus. They cited the loss of protection from the rain (removal of a leaf canopy above the cocoon), and falling to the ground (support line failure) as reasons why the flocculent silk cocoons of this spider failed. Overall, the lack of any effect on the incidence of fungal attack through manipulation of the covers and suspension systems of M. lemniscata and A. aurantia cocoons is surprising, particularly

since these components presumably perform the same functions as the leaf layer and support system of N. clavipes cocoons. These results may be partially explained by differences in the cocoons of the three species. The cocoons of M. lemniscata and A. aurantia have dense covers, and layers of flocculent silk between the cover and the egg mass. While the covers of both these cocoons are wettable, the flocculent silk layer is not. The cocoon of N. clavipes is composed primarily of a basket-like mesh, with little or no flocculent layer between the eggs and the mesh. The eggs in M. lemniscata and A. aurantia cocoons with damaged covers are still protected from water (and fungal spores?) by their flocculent silk layer (which was not damaged in this study). The mesh cocoons of N. clavipes, which are also wettable, have no flocculent layer to turn water away from the egg mass once their protective leaf canopy is gone. Other explanations for this difference, such as a layer of spherical granules on the surface of the eggs of these two species which repel water (Austin and Anderson 1978, Grim and Slobodchikoff 1978, 1982, Humphreys 1983), or relatively short developmental periods are not adequate, since all three spiders share these traits.

The differences in the incidence of drowning between M. lemniscata and A. aurantia cocoons in the egg and spiderling stages (see Tables 5-2 and 5-4) are probably related to differences in the size of these cocoons, and the thicknesses of their flocculent silk layers. The cocoons of M. lemniscata are small, and are worked down into the soil by rain action when placed on the

ground. In this location, the cocoons are in constant contact with soil moisture. Argiope aurantia cocoons are relatively large (see Figs. 2-1 and 2-2), and remain on the surface if they fall to the ground. In this position, the area of the cocoon contacting the soil is minimized, which probably allows the cocoon to dry out between exposure to rain or submersion.

The spiderlings in M. lemniscata cocoons are also packed together tightly, with no room to move about within the cocoon. In addition, the flocculent silk layer in these cocoons is relatively thin. Fungal infection, once established, can spread more easily to all the spiderlings within the cocoon. The thicker flocculent silk layer in the cocoons of A. aurantia provides protection from water entering the cocoon, even when the cover is damaged. The large size of these cocoons also allows the spiderlings to move about in the cocoon, which may further reduce the probability of infection moving through the mass. Indeed, in cocoons damaged naturally or modified by me, the spiderlings are almost always appressed against the cocoon cover opposite the site of the damage.

The differences between the overall levels of fungal attack on the cocoons of these two spiders are also interesting. The cocoons of M. lemniscata are covered by layers of discarded orb-web that contains detritus composed primarily of prey remains. These remains may provide a high quality medium for fungal spores to germinate on, and from them, extend their hyphae into the cocoons. On occasion, I have observed M. lemniscata cocoons completely enswathed by a fuzzy layer of grey or white fungus. I have also had M. lemniscata

cocoons that were stripped of their outer layer of silk (see Fig. 2-1c) attacked by fungi in the laboratory. In contrast, A. aurantia cocoons, which have a naked cover with an almost lacquered surface finish, are never covered by fungus. In fact, it is rare to find small patches of fungus on the covers of these cocoons at all, even after they have been lying on the ground for 90 days (see Table 5-4).

Spiders produce a variety of silks and associated materials in a number of different glands located in their abdomens (Witt et al. 1968, Mullen 1969, Foelix 1982). One of these, the aggregate gland, produces the glue-like material found on the catching spiral of orb-webs. Schildknecht et al. (1972) have demonstrated that this glue-like material contains nitrates (KNO_3), phosphates (KH_2PO_4), and pyrrolidines ($C_4H_2NO_2$). They suggest that one of the functions of these compounds is to protect the web from bacterial and fungal attack. If spiders are protecting their webs from such attack, it seems reasonable that they would protect their cocoons, which represent a much greater expenditure of energy and time, as well. Given that these compounds can be manufactured in the silk glands associated with web building, it seems likely that the tubiliform and aciniform glands associated with cocoon production may also able to manufacture similar compounds, so they can be applied to the covers of cocoons.

The preceeding Chapters III, IV, and V have both considered and demonstrated the role of the cocoon, or its various parts, in limiting the effects of temperature extremes, dessication, and

fungal attack on the egg and spiderling stages of M. lemniscata and A. aurantia. However, many predator groups have specialized on the eggs of spiders, and it is probable that cocoons also function to control their attacks. This possibility is considered in Chapter VI.

CHAPTER VI
THE ROLE OF THE COCOON IN LIMITING EGG AND SPIDERLING PREDATORS

Introduction

A major portion of modern ecology is concerned with the relationship between heterotrophic organisms and their food supplies. Such interactions (e.g., predator vs. prey, host vs. parasite) occur both in ecological time, and in evolutionary time (Brower and Brower 1972, Dawkins and Krebs 1979). As such, natural selection may be presumed to act within interacting populations to optimize both the ability to acquire resources (Schoener 1971, Pyke et al. 1977), and the ability to avoid becoming the acquired resources of similarly-selected organisms of higher trophic levels. Within this context, the strategy of any host organism should be to protect itself, or its offspring, from the effects of predator or parasite attack through processes or behaviors which limit the types and numbers of attackers that are capable of using it. Ideally, the strategy should result in the total exclusion of all the attackers. In reality, their effect is only partially reduced due to the reciprocal nature of the interaction over evolutionary time.

Spiders deposit their eggs in one or more discreet clutches. These clutches can be extremely large (up to 2000 eggs; Kaston 1948). The individual eggs within the clutch are also

quite large when compared to eggs of other groups such as insects. The eggs are lipid rich and represent a considerable amount of energy (Anderson 1978). In addition, during the reproductive season, clutches may occur in large numbers in the habitat and may be relatively conspicuous. They therefore represent a potential and highly desirable resource for many predators and parasites. Indeed, insects from a number of groups have specialized on spider eggs (Auten 1925, Eason et al. 1967, Evans 1969, Askew 1971, Austin, In press).

All spiders deposit their eggs in some form of silken cocoon (Turnbull 1973). For many spiders this structure represents the sum total of maternal care bestowed on the eggs by the female spider. The large and diverse number of predators attacking cocoons, and the wide range in complexity of cocoon architecture (McCook 1890, Kaston 1948) have led to speculation that the primary function of the cocoon is to protect the eggs and spiderlings from attack (Austin and Anderson 1978, Robinson 1980). Austin (In press) recently reviewed the literature on cocoon attack by egg predators, and proposed that the wide diversity of cocoon types arose because spiders have attempted to reduce the total number of predators that can use their cocoons by forcing them to "specialize" on a particular cocoon type. The predators have responded in evolutionary time, and the relationships between cocoons and their attackers that we observe today can be attributed to a "coevolutionary arms-race" (Dawkins and Krebs 1979). While some observations have been reported on parasite difficulty in entering

cocoons (Kaston and Jenks 1937), there is still no evidence that cocoons, or the various layers comprising them, function to turn away or reduce the success of specific parasites or predators.

In this chapter, I investigate the roles that the suspension systems, outer covers, and internal flocculent silk layers of the cocoons of Mecynogea lemniscata Walckenaer and Argiope aurantia Lucas (Araneidae) play in controlling the access of predators to the eggs and spiderlings within. If the suggestions of various researchers, and in particular Austin (In press), are correct, these cocoons should demonstrate defenses which reflect the manner in which their predators attempt to introduce themselves or their offspring into the cocoon.

Materials and Methods

Population Data

The numbers and kinds of parasites and predators attacking the cocoons of M. lemniscata and A. aurantia were determined by collecting cocoons in the field and returning them to the laboratory where they were opened and scored for parasites. Scoring was relatively easy since each parasite leaves distinctive evidence in the cocoon such as the type of hole in the cover, or remains such as pupal cases, shed exuviae, or eggs. The M. lemniscata cocoons were collected in late August in 1981 to 1983 after the eggs in the last cocoons laid had hatched. A single sample of A. aurantia cocoons was collected in late October in 1981. In 1982 and 1983, a

different 31 m of a 400 m stretch of roadside hedgerow was sampled every two weeks. For each sample, all of the cocoons in the 31 m section were collected. In 1982, the cocoons were collected from August through November; in 1983, from August through October.

In addition to these data, specific information was also collected regarding attacks on A. aurantia cocoons by ichneumonid wasps and chloropid flies. For the ichneumonid attacks, these data included two indices relating the distance of the egg mass to the cocoon cover along the X and Y axis. These indices were calculated by first measuring the following four variables: egg mass length, egg mass width, cocoon length, and cocoon width (Fig. 6-1). These values were then used in the following formulas:

$$\text{Distance to the egg mass from the cocoon cover (x-axis)} = \frac{(\text{Cocoon Width} - \text{Egg Mass Width})}{2}, \text{ and}$$

$$\text{Distance to the egg mass from the cocoon cover (y-axis)} = \frac{(\text{Cocoon Length} - \text{Egg Mass Length})}{2}.$$

These two measures were compared to the average ovipositor length of the ichneumonid to predict where the wasp might prefer to attack the cocoon. The predicted preference was checked by examining the shells of attacked cocoons collected in the field for the distribution of ovipositor drill holes. Data on the number of cocoons that the wasp attacked without ovipositing, and the distribution of support line "deltas" (the structure on the cocoon surface the support lines emanate from; McCook 1890) were also

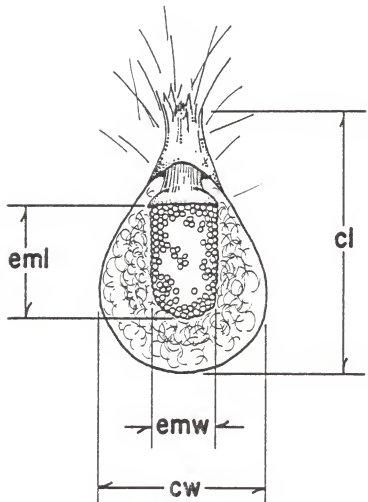


Fig. 6-1. A schematic view of an Argiope aurantia cocoon illustrating the four measurements; cocoon length (cl), cocoon width (cw), egg mass length (eml), and egg mass width (emw) taken to determine the position of the egg mass in relation to the cocoon cover.

collected. For the chloropid fly attacks, the number of cocoons successfully attacked (producing pupae), the number of cocoons successfully attacked in conjunction with another predator, and the number of cocoons unsuccessfully attacked (eggs laid on the cocoon surface but no pupae produced) were recorded.

The relationship between the size of an A. aurantia cocoon and the number of eggs it contained was established by measuring a number of cocoon dimensions and counting the spiderlings in 40 cocoons. Figure 6-2 shows that there is a strong relationship (r^2 = 0.90) between the diameter of the cocoon and spiderling number. This relationship was used to estimate the original number of eggs in attacked cocoons. The percentage of eggs surviving the attack, a measure of the damage caused by a given predator, was then calculated by the following:

$$\text{Percentage of Eggs Surviving Parasite Attack} = \frac{\text{No. of Survivors}}{\text{Estimated No. of Eggs}} \times 100.$$

The relationship of cocoon size to egg number was not calculated for M. lemniscata because all of the eggs in a cocoon are utilized when attacked by its egg predators.

Field Experiments

The roles of suspension systems and cocoon covers in controlling egg predator attacks were investigated by modifying these components in the field and assessing the effects of their change on egg hatching success and spiderling survival. The cocoons

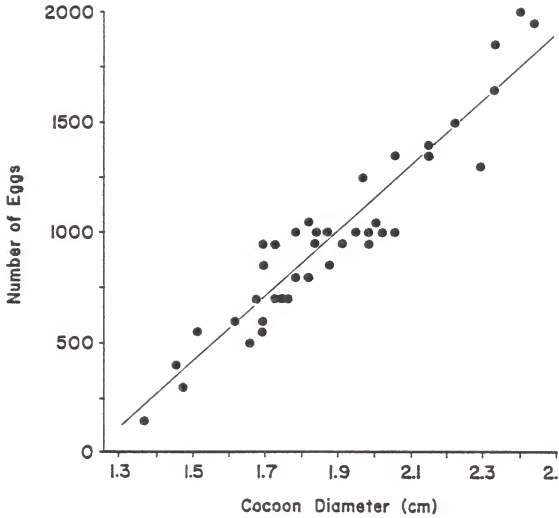


Fig. 6-2. The relationship (Y = 1522.2X - 1886.9; n = 40) between the diameter of Argiope aurantia cocoons and the number of spiderlings (eggs) therein. The coefficient of determination (r^2) for the relationship is 0.90.

used for these modifications were either produced in the laboratory, or collected in the field. They were assigned to the experimental groups listed below. The cocoons in all the experimental groups were marked either by flagged stakes placed beneath them, or by flagging in the vegetation.

Vegetation contact. The function of cocoon support lines as a deterrent to arboreal predators was examined by repositioning cocoons so that they contacted the vegetation. This was done only for M. lemniscata cocoons and was accomplished by tying cocoon strings to branches with their suspension lines. This mimicked the position of cocoons whose suspension systems had collapsed normally.

Ground placement. The role of the suspension system in keeping cocoons off of the ground and away from terrestrial predators was investigated by placing the cocoons of both species on the ground in open-topped wire corrals. These corrals allowed cocoons to be attacked but prevented them from being washed away in the rain. The corral used for A. aurantia cocoons was constructed of hardware cloth (1/4" mesh) and was 12.5 cm in diameter and 5 cm in height. The corral for M. lemniscata cocoons was constructed of aluminum window screen and was 5 cm in diameter and 5 cm in height. The corrals were located below sites where cocoons had been collected previously.

Cover removal. The function of the cocoon cover in limiting predator attack was examined by removing approximately 25% of the cocoon cover with a razor blade. Individual cocoons of M. lemniscata were modified in the cocoon string and the string was

left suspended in place at the web site. Female spiders treated these modified cocoons normally. The laboratory reared cocoons of A. aurantia were modified and attached to the arms of a support system using alligator clips. The support systems were placed in the vegetation where normally oviposited cocoons were hanging. They held the cocoons approximately 1 m off of the ground (the average cocoon height as determined by collecting).

Cover removal control. This group was to control for the possible contaminating effects of the alligator clip used in the apparatus to suspend A. aurantia cocoons. Clips were attached to cocoons hanging normally in the habitat and the cocoons were observed for any effect.

Control. Control cocoons were subjected to no structural intervention. These cocoons controlled for handling effects in the ground placement, vegetation placement, and cover removal groups.

Bird damage. These A. aurantia cocoons were subjected to no mechanical modification. They were marked and collected after 150 days in the field to determine whether bird predation increases later in the year after the plants lose their leaves (see also Tolbert 1976). They were compared to the control group.

Laboratory Experiments

The role of the flocculent silk layer in the cocoons of A. aurantia as a barrier to predator attack was tested in the laboratory by placing the eggs of Tromatobia ovivora rufopectus (Cresson) (Ichneumonidae) at two depths in the cocoon: 1) just under

the cover, and 2) on the host egg mass. Successful parasitism was scored as the number of ichneumonid larvae found in the host egg mass just prior to pupation.

The wasps were maintained in the laboratory at 23-25° C and 50-60% RH. They were provided with white refined sugar, a mixture of honey and yeast, and water. Colony size was maintained by the addition of new wasps collected from the field. Their eggs were obtained by allowing a number of wasps to attack a cocoon produced in the laboratory. The cocoon was then opened, and the white, elongate wasp eggs were removed using a fine brush and forceps. Known numbers of these eggs were then transferred to other laboratory produced cocoons 1-3 days old, and placed in either of the two test locations.

The cocoons were obtained from spiders held in the laboratory in 50 x 50 x 10 cm cages (Witt 1971) or in 500 ml jars with screen tops. Oviposition and cocoon construction in both of these enclosures was normal.

Results

Field Experiments

The cocoons of *M. lemniscata* are attacked in the egg stage by two major predators, a *Tetrastichus* sp. wasp (Eulophidae) and the neuropteran *Mantispa viridis* Walker (Mantispidae) (Hieber 1984) (Table 6-1). Both of these predators utilize all of the eggs in a cocoon during their attacks. However, they attack the cocoons in

Table 6-1. Numbers of Mecynogea lemniscata cocoons attacked by the eulophid wasp Tetrastichus sp., the mantispid Mantispa viridis, and ants/ unknown predators for the years 1981 to 1983. The cocoons were collected in late August in 1981 and 1982 at the end of the reproductive season, and in July, August, and December in 1983. The percentages of attacked cocoons are in parentheses.

Year	Sample Size	Total No. Attacked	Eulophid Wasp[a]	Mantispid[b]	Ants/ Unknown[c]
1981	290	26	21 (80.8%)	0 (0%)	5 (19.2%)
1982	252	29	17 (58.6%)	5 (17.2%)	7 (24.1%)
1983					
July	148	13	10 (76.9%)	2 (15.4%)	1 (7.7%)
Aug.	97	14	12 (85.7%)	0 (0%)	2 (14.3%)
Dec.	308	64	32 (50.0%)	12 (18.8%)	20 (31.2%)

[a] Cocoons contain either larvae, prepupae, and/or shed exuviae with emergence holes.

[b] Cocoons contain either a larva, a pupa, or a pupal case and emergence hole.

[c] Cocoons are characterized by a large chewed hole, and the absence of the flocculent silk layer, pupal cases, pupae, shed exuviae, or parasite.

different ways. Mantispa viridis deposits its eggs in the habitat, removed from the host, and the emerging triungulid larvae actively search out and burrow into previously constructed cocoons. These larvae are obligate cocoon attackers, as opposed to the mantispid larvae that ride on female spiders and attack the egg mass just prior to cocoon construction (see Redborg and McLeod, In press, for a review of Mantispid biology). The Tetrastichus wasp either deposits eggs into the cocoon, or into the upper layers of the cocoon cover where the emerging larvae burrow through the cocoon and attack the egg mass (Austin, In press). Both the wasp and the mantispid are never found together in the same cocoon. The cocoons of M. lemniscata are also occasionally attacked by ants, which also remove all of the eggs or spiderlings.

The single line suspension system of M. lemniscata cocoons functions to prevent predation on the egg stage. Egg predation was significantly greater than control for both the cocoons placed on the branches ($X^2 = 47.40$, df = 1, $p < 0.001$) and those placed on the ground ($X^2 = 23.49$, df = 1, $p < 0.001$) (Table 6-2). In both cases, the principle predator appeared to be ants. Modification of the cocoon cover also had a significant effect on egg predation ($X^2 = 38.67$, df = 1, $p < 0.001$). In this case, however, the principle predator was not ants, but the mantispid M. viridis. In no case did the wasp attack any manipulated cocoons containing eggs, suggesting that the position of the cocoon in the web or the integrity of the cocoon cover are important to the wasp.

Table 6-2. The effect of modification of the cocoon suspension system and cover on the incidence of predator attack on the eggs of Mecynogea lemniscata. All cocoons were collected after 30 days.

Experimental Modification	Sample Size	Successful Survival	No. Cocoons Attacked	% Cocoons Attacked
Control	175	153	22[a]	12.6%
Vegetation Contact	24	6	18[b]	75.0%
Ground Placement	26	12	14[b]	53.8%
Cover Removal	32	12	20[c]	62.5%

[a] Of the 22 cocoons attacked, 2 were attacked by ants/ unknown predators, 19 by the eulophid wasp Tetrastichus sp., and 1 by the mantispid M. viridis.

[b] In both cases the cocoons were attacked by ants/ unknown predators.

[c] All 20 cocoons were attacked solely by the mantispid M. viridis.

The effect of the suspension system in protecting M. lemniscata spiderlings from predators was not as pronounced (Table 6-3). There were no differences in predation between the Control group and either the cocoons placed on the ground for 45 days or the cocoons placed in contact with the vegetation. The cocoons placed on the ground for 90 days, however, were preyed upon at significantly higher levels ($X^2 = 70.40$, df = 1, $p < 0.001$). These results probably reflect the generally lower densities of ants foraging on the vegetation and ground late in the year (pers. ob.). Cover removal also had no significant effect on spiderling predation when compared to control, again because the the cocoons are inaccesible on their support line.

The eggs of A. aurantia are attacked by four primary predators; the wasp T. ovivora rufopectus (Ichneumonidae), the neuropteran M. viridis, and the flies Pseudogaurax signata (Loew) (Chloropidae) and Megaselia sp. (Phoridae) (Table 6-4). Of these, the two most common predators are the ichneumonid and the mantispid. These are obligate egg predators and probably account for most of the initial attacks in cocoons attacked by multiple predators. The attack behavior of the mantispid has been previously discussed. The ichneumonid T. ovivora rufopectus attacks A. aurantia cocoons by inserting its long ovipositor through the cover into the flocculent layer. Its eggs are deposited on or near the host egg mass, and the emerging larvae make their way to the host eggs and burrow into the mass to feed.

Table 6-3. The effect of modification of the cocoon suspension system and cover on the incidence of predator attack on the spiderlings of Mecynogea lemniscata. All cocoons were collected after 90 days, except for those placed on the ground. They were collected after 45 and 90 days.

Experimental Modification		Sample Size	Successful Survival	No. Cocoons Attacked	% Cocoons Attacked
Control		259	239	20[a]	7.7%
Vegetation Contact		77	71	6[a]	7.8%
Ground Placement	(45)	19	17	2[a]	10.5%
	(90)	32	11	20[a]	62.5%
Cover Removal		34	32	2[a]	5.9%

[a] All attacks were by ants/ unknown predators.

Table 6-4. Numbers of Argiope aurantia cocoons suspended in the vegetation which were successfully attacked by the ichneumonid Tromatobia ovivora rufopectus, the mantispid Mantispa viridis, the chloropid fly Pseudogaurax signata, the phorid fly Megaselia sp., and birds for the years 1981 to 1983. The percentages of attacked cocoons are in parentheses. The cocoons were attacked to a lesser extent by ants [1 cocoon (1.6%) in 1981, 2 cocoons (1.1%) in 1982], and moth larvae [3 cocoons (1.6%) in 1982]. Forty-two of the 185 cocoons (23.0%) collected in 1982 were also attacked by unknown predators and showed varying degrees of cover damage. The cocoon sample for 1981 was collected in late October. In 1982 and 1983, the cocoon samples were collected approximately every two weeks during the reproductive season (August to November).

Year	Sample Size	Total No. Attacked	Ichneumonid Wasp[a]	Mantispid[b]	Chloropid Fly[c]	Phorid Fly[d]	Bird[e]
1981	63	16[f]	13 (81.2%)	1 (6.2%)	3 (18.8%)	2 (12.5%)	0
1982	185	89[g]	34 (38.2%)	27 (30.3%)	42 (47.2%)	4 (4.5%)	17 (19.1%)
1983	90	9[h]	2 (22.2%)	5 (55.6%)	1 (11.1%)	0	1 (11.1%)

[a] Attack characterized by the presence of oviposition holes, eggs, larvae, and pupal cases.

[b] Attack characterized by the presence of pupal cases and adults.

[c] Attack characterized by the presence of eggs on the cocoon cover or in the flocculent silk layer, larvae, pupal cases, and adults.

[d] Attack characterized by the presence of larvae, pupal cases, and adults.

[e] Attack characterized by a large percentage of the cocoon cover (> 10.0%) torn away, and the partial or complete removal of the cocoon contents.

[f] Of the 16 cocoons attacked, 11 were by the ichneumonid alone, 1 by the mantispid alone, and 1 by the phorid fly alone. The remaining 3 cocoons were multiply attacked by the ichneumonid and chloropid fly (2 cocoons), and the phorid and chloropid flies (1 cocoon).

[g] Of the 89 cocoons attacked, 24 were attacked by the ichneumonid (I) alone, 11 by the mantispid (M) alone, 17 by the chloropid fly (C) alone, 2 by the phorid fly alone (P), and 5 by birds (B) alone. No cocoons were attacked by the moth (Mt) alone. The remaining 30 cocoons were attacked by more than one predator in the following combinations: (I-M, 2 cocoons), (I-C, 4 cocoons), (I-B, 1 cocoon), (M-C, 6 cocoons), (M-B, 1 cocoon), (C-B, 5 cocoons), (C-Mt, 2 cocoons), (B-Mt, 1 cocoon), I-M-C, 3 cocoons), (M-C-P, 1 cocoon), (M-C-B, 3 cocoons), and (C-P-B, 1 cocoon).

[h] Of the 9 cocoons attacked, 2 were attacked by the ichneumonid alone, 5 by the mantispid alone, 1 by the chloropid fly alone, and 1 by birds alone.

The status of P. signata is less clear. This fly deposits eggs on cocoon surfaces. The eggs hatch and the emerging larvae push their way through the cover into the cocoon (Kaston and Jenks 1937, Kessel and Kessel 1937, Hickman 1970). The literature suggests that chloropid flies are obligate spider egg parasites (see Austin, In press), a fact supported by the large number of A. aurantia cocoons attacked by this fly in 1982. However, only 17 of 42 cocoons were singly attacked by this fly (Table 6-4). The remaining cocoons were attacked along with other predators (particularly mantispids), and in many cases the fly deposited its eggs in the emergence holes of these previous attackers. In addition, Hall (1937) lists this fly as attacking the egg masses of the praying mantis. This suggests that this fly is a facultative egg predator that attacks eggs in any container, as well as utilizing dead or damaged eggs from other attacks when located. The phorid is found alone in cocoons approximately 50% of the time and it is probably an obligate egg predator, attacking cocoons in the same manner as P. signata.

The observed levels of egg predation for T. ovivora rufopectus, P. signata, and M. viridis in this study are similar to the levels of attack reported by Enders (1974) and Tolbert (1976) for A. aurantia cocoons. The A. aurantia cocoons in this study were also attacked by birds, ants, and moth larvae, although it is unclear whether these attacks occured in the egg or spiderling stage. The level of bird attack was lower (9%) than that found by Tolbert (35-50%). Argiope aurantia cocoons containing spiderlings are attacked by ants and other spiders (particularly salticids which

use damaged cocoons as retreats), and by small rodents if cocoons fall to the ground.

The amount of damage done to the eggs in an A. aurantia cocoon by each of the four primary predators varies greatly (Table 6-5). The ichneumonid, on average, does the greatest amount of damage, destroying approximately 90% of the host eggs. By themselves, the chloropid fly and the mantispid attack roughly the same number of cocoons. However, the average mantispid attack damages approximately 20% more eggs than the average chlorpid attack. The phorid fly destroys approximately 97% of the eggs in a cocoon. Birds also damage the contents of the cocoon heavily (74%), but the damage is usually done in the spiderling stage.

Tromatobia ovivora rufopectus was successful in attacking 34 cocoons in 1982 (see Table 6-4). However, an examination of the covers of 167 cocoons collected that year (the other 18 covers were to damaged to inspect) for ichneumonid oviposition holes indicated that 92 cocoons were actually sampled by the wasps. Thus, 58 cocoons were sampled but had no eggs deposited in them, presumably because they were in the wrong stage for attack (Vinson 1976). The other 75 cocoons were either never found by the ichneumonids, or were found and rejected based on criteria which did not require insertion of the ovipositor to determine.

The number of cocoons containing pupal cases of P. signata was also not a valid measure of the total number of cocoons attacked by this fly (see Table 6-4). Of the 69 cocoons in 1982 with attached P. signata eggs, 27 (39.1%) were apparently unsuccessful in that

Table 6-5. The mean percentage of eggs which survive in an Argiope aurantia cocoon attacked solely by the ichneumonid Tromatobia ovivora rufopectus, the mantispid Mantispa viridis, the chloropid fly Pseudogaurax signata, the phorid fly Megaselia sp., or birds. SD is in parentheses.

Parasite	No. Cocoons Sampled	Percent Eggs Surviving
Ichneumonid	35	10.2 (13.7)
Mantispid	15	39.1 (27.6)
Chloropid Fly	15	63.7 (35.6)
Phorid Fly	4	4.7 (9.5)
Birds	16	26.4 (28.3)

emerging larvae failed to gain entrance into the cocoon (no pupal cases inside the cocoon). The remaining 42 cocoons were successfully attacked and can be divided into two groups; 17 cocoons attacked by the fly alone, and 25 cocoons attacked by the fly and one or more other predators. Of the 17 singly attacked cocoons, 13 had eggs on the surface and a fewer number of pupae inside, 2 had more pupae than eggs present, and 2 had pupae and no eggs present. Of the remaining exhibiting multiple attacks, 11 had eggs on the outside and inside of the shell and contained less (8 cocoons) or more pupae (3 cocoons) than eggs. The other 14 cocoons had pupae, but no evidence of eggs could be found because the cocoon and its contents were heavily damaged.

The large number of cocoons attacked by P. signata in conjunction with other predators suggests that shell damage may be advantageous to this fly (see Table 6-4). Indeed, the average rate of success (number of pupae/ number of eggs X 100) for the cocoons attacked by the fly alone was 29.8% (SD = 30.2%) (based on the 13 cocoons which had visible eggs). The average rate of success for the flies which attacked cocoons with other predators was 82.7% (SD = 19.74%) (based on 11 cocoons; the 3 with more pupae than eggs were counted as 100% successful). This level of success is significantly greater ($t = 10.05$, $df = 22$, $p < 0.001$) than that achieved by P. signata attacking cocoons alone.

It is difficult to determine whether the success rates for mantispids and phorid fies attacking A. aurantia cocoons are due to an inability to locate the cocoons, or to the inability of the

respective larvae to penetrate the cocoon cover. The large increase in successful mantispid attacks on artificially damaged M. lemniscata cocoons suggests that mantispid larvae are generally abundant and probably have no trouble locating cocoons, but have difficulty penetrating the dense cocoon cover. This suggests that the cover of A. aurantia cocoons is also responsible for the relatively low rate of successful mantispid attack. Presumably, the larvae of the phorid fly are also hindered by the cover, although this is a rare parasite and the low numbers of successful attacks may be a reflection of low numbers of searching parasites. It seems likely that birds, once they find a cocoon, have little trouble in exploiting it.

In A. aurantia cocoons, the egg mass is closest to the cocoon cover at its top edge, farthest from the cocoon cover at its bottom, and approximately the same distance as the average ovipositor length from the cocoon cover in the middle of the cocoon (Table 6-6). The cocoons are suspended in the vegetation by a cloud of lines emanating from suspension line "deltas" on the surface of the cocoon (see Fig. 2-2a). There are significantly more of these deltas, and thus significantly more lines, in the middle third of the cocoon surface than in either the upper ($t = 4.48$, $df = 140$, $p < 0.001$) or lower third ($t = 156.40$, $df = 140$, $p < 0.001$) (Table 6-7). The distribution of ichneumonid drill holes matches the delta distribution; there are significantly more holes in the middle third than in either the upper ($t = 4.69$, $df = 166$, $p < 0.001$) or lower third ($t = 3.92$, $df = 166$, $p < 0.001$) of the cocoon (Table 6-7).

Table 6-6. Mean cocoon diameter, cocoon length, egg mass diameter, egg mass length, distance to the egg mass (X-Axis), and distance to egg mass (Y-Axis) for Argiope aurantia cocoons, and mean ovipositor length for the ichneumonid Tromatobia ovivora rufopectus. The two distance variables indicate the length of an ovipositor needed to deposit eggs directly on the surface of the host egg mass. SD is in parentheses.

Variable	Sample Size	Mean (mm)
Cocoon Diameter	25	19.2 (2.2)
Cocoon Length	25	24.4 (2.4)
Egg Mass Diameter	25	10.2 (1.4)
Egg Mass Length	25	11.1 (1.4)
Distance to Egg Mass from cover: X-axis	25	4.5 (0.7)
Distance to Egg Mass from cover: Y-axis	25	6.7 (1.2)
Ovipositor Length	57	3.9 (0.5)

Table 6-7. The mean number of suspension line deltas and oviposition holes of the ichneumonid Tromatobia ovivora rufpectus in the upper, middle, and lower thirds of the cover of Argiope aurantia cocoons. SD is in parentheses.

	Sample Size	Upper Third	Middle Third	Lower Third
Suspension Line Deltas	71	18.7 (6.2)	22.3 (9.2)	3.9 (3.7)
Ichneumonid Oviposition Holes	84	2.4 (3.7)	9.5 (13.4)	3.4 (5.0)

The location of the egg mass within the cocoon and the distribution of drill holes suggests that the ichneumonid prefers to attack the cocoon in this specific area.

For A. aurantia, egg predation due to the cocoon falling to the ground was not statistically different from the control in terms of the number of cocoons attacked (Table 6-8). However, the individual survival of eggs in each cocoon was reduced substantially. All of the cocoons on the ground discovered by predators suffered 100% egg mortality as compared to about 59.4% mortality for cocoons remaining in place in the vegetation. The cocoons on the ground that escaped attack were buried by falling leaves and were presumably hidden from predators. The level of predation on eggs in cocoons with modified covers was also not significantly different from the Control group. However, in all cases the cocoons were attacked by the chloropid fly P. signata, further suggesting that damaged cocoons appeal to this egg predator. The lack of mantispids in the modified cocoons is most likely related to the apparatus used to suspend the cocoons, which prevented the larvae from locating the cocoons, and not because of their inability to use them.

The effect of cover modification also had no effect on predation in the spiderling stage when compared to the Control group (both controls were not significantly different from one another) (Table 6-9). Placement on the ground, mimicking suspension failure, resulted in significantly greater predation ($X^2 = 24.37$, df = 1, p on the ground (5.9%) was also much lower then for spiderlings in

Table 6-8. The effect of modification of the cocoon suspension system and cover on the incidence of predator attack on the eggs of Argiope aurantia. All cocoons were collected after 30 days.

Experimental Modification	Sample Size	Successful Survival	No. Cocoons Attacked	% Attacked Attacked
Control	21	10	11[a]	52.4%
Ground Placement	10	2	8[b]	80.0%
Cover Removal	17	10	7[c]	41.2%

[a] Of the 11 cocoons attacked, 8 were attacked by the chloropid fly P. signata, 8 were attacked by the mantispid M. viridis, 1 by the phorid fly Megaselia sp., 1 by the ichneumonid T. ovivora rufopectus, and 5 by birds.

[b] Rodent (mice) damage. The cocoon covers were shredded and the contents destroyed.

[c] All 7 cocoons were attacked solely by the chloropid fly P. signata.

Table 6-9. The effect of modification of the cocoon suspension system and cover on the incidence of predator attack on the spiderlings of Argiope aurantia. All cocoons were collected after 90 days, except for those in the bird damage group. They were collected after 150 days.

Experimental Modification	Sample Size	Successful Survival	No. Cocoons Attacked	% Cocoons Attacked
Control	23	20	3[a]	13.0%
Cover Removal Control	15	14	1[b]	6.7%
Ground Placement	19	2	17[c]	89.5%
Cover Removal	21	20	1[d]	4.8%
Bird Damage	23	15	8[e]	34.8%

[a] Bird damage. Of the 3 cocoons, 2 had part of their cover removed, and 1 had cover damage and the contents removed.

[b] Bird damage.

[c] Rodent (mice) or bird damage. Characterized by the cover being shredded and the contents removed.

[d] Bird damage. Contents removed from the cocoon.

[e] Bird damage. Of the 8 cocoons, 2 were removed completely, 5 had 25-50% of their covers removed, and 1 had the cover damaged and the contents removed.

cocoons in the vegetation (98.4%). Predation by birds increased during the latter part of the season, and while the numerical increase was not significant, the average level of individual survival was lower (76.6%).

Laboratory Experiment

The mean percentage of success for T. ovivora rufopectus eggs placed just under the cocoon shell was 62.5% (SD = 13.8%, n = 4). For the parasite eggs placed on the surface of the A. aurantia egg mass the mean percentage of success was 85.4% (SD = 11.2%, n = 3). These two levels of success were not significantly different from one another ($0.10 > p > 0.05$). Nevertheless, a trend is indicated and a test with larger sample sizes would probably yield significance.

Discussion

The suspension systems of the cocoons of both M. lemniscata and A. aurantia function in two major ways. First, they keep the cocoon isolated from contact with the surrounding vegetation and, consequently, isolated from generalist pedestrian predators. The low rates of attack by ants on the suspended cocoons of both spiders suggest that few non-flying predators are willing or able to venture out on the silk suspension lines. This is supported by the significant rise in predation, particularly in the egg stage, for M. lemniscata cocoons placed in contact with the vegetation. The three field collected A. aurantia cocoons attacked by ants were also

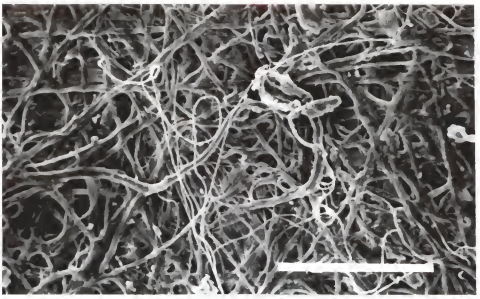
cocoons that had contacted the vegetation because of suspension system failure (see Table 6-4). Second, the suspension system functions to maintain the position of the cocoon within the proper microhabitat or vegetational layer. Parasites (Moore 1977) and pedestrian predators (Robinson 1980) may be distributed predictably in the habitat, and cocoons that change position due to structural failure may move into strata where they are available to new predators or are generally easier to locate. Indeed, cocoons of M. lemniscata suffered increased rates of predation from ants, while those of A. aurantia were attacked heavily by small rodents [see also Robinson and Robinson (1976)] when they were placed on the ground. The importance of maintaining position is further emphasized by the difference in average individual survival for A. aurantia cocoons that were left in position in the vegetation (59-98%), and for those that were placed on the ground (0-5%).

The literature suggests that parasitic flies are fairly common in cocoons with loosely woven covers, but are not found often in cocoons with hard or dense covers (Eason et al. 1967, Muma and Stone 1971, Austin, In press). The results of cover modification on M. lemniscata cocoons supports this view. The triungulid larvae of M. viridis had no trouble crossing the silk suspension line or finding the correct line to the cocoon in the maze of the tangle web (Hieber 1984). However, the dense cover prevented the larvae from successfully entering the cocoon (see also Kaston and Jenks 1937). The high percentage of unsuccessfully attacked cocoons with chloropid fly eggs on them, and the significant increase in

successful attacks by P. signata larvae on A. aurantia cocoons damaged by the attacks of other parasites suggests that the covers of A. aurantia cocoons are also a barrier to attack by larvae. From this, I concluded that the cocoon cover functions primarily to prevent the access of actively searching mantispid and dipteran larval stages. Austin (In press; citing an unpublished author) points out that female wasps in the genera Tetrastichus and Eurytomus (Eulophidae) oviposit into the topmost layers of cocoons. The emerging first instar larvae then burrow through the cocoon wall and attack the host eggs. If the Tetrastichus wasp in this study utilizes a similar method of attack, the dense cover of M. lemniscata cocoons cover may make entrance difficult for the attacking larvae. Difficulty in entering the cocoon may account for the relatively low rate of parasitization (see Table 6-1).

The greater success of mantispids in attacking A. aurantia cocoons (5-14%) over M. lemniscata cocoons (0-4%) suggests that A. aurantia cocoons do not present as difficult a barrier to attacking larvae. This may be related to the structure of the cocoon itself since the covers of A. aurantia cocoons are less tightly woven than those of M. lemniscata (see Fig. 6-3). However, the architecture of these two cocoons may also reflect broader reproductive strategies. Adult female M. lemniscata are preyed upon heavily by mud-daubing wasps (pers. ob.) and by kleptoparasitic Argyrodes spp. (Araneae: Theridiidae) (see also Trail 1980, Wise 1982) in the early to middle part of their reproductive season. They are therefore probably under some constraints to produce

A.



B.

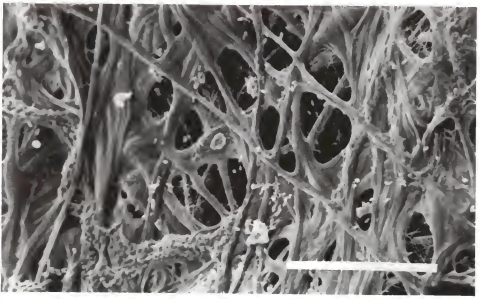


Fig. 6-3. The covers of the cocoons of Mecynogea lemniscata (A) and Argiope aurantia (B) comparing the difference in the tightness of the weaving. The scale line in each equals 120 µm. Both cocoons were plated with 75 Å of gold and observed using secondary electrons.

clutches as quickly as possible. This may account for the small clutch size of the spider. Since the probability of only producing one or a few small clutches is high, these should be protected as well as possible, particularly since successful predator attack on M. lemniscata cocoons is always 100% fatal. In contrast, A. aurantia is a large spider when mature, and few predators attack it. This spider's reproductive season is timed with the early fall peak in orthopteran prey, and the relative abundance of food allows the average spider to produce 1-3 huge clutches of 800-2000 eggs. In the midst of abundant prey, allocating a percentage of the egg mass to those predators using a larval attack might be less expensive than the increase in time and energy involved in making a cocoon totally impenetrable. The relativly low percentage of eggs lost to attacking mantispids and chloropid flies (30-40%) in comparison to those lost in a successful ichneumonid attack (90%) suggests that this is a viable alternative (see Table 6-5).

The advantages of the cover as a physical barrier to attack disappear when the cocoon is attacked by wasps with long ovipositors. This is because the cover can be circumvented by the ovipositor, and the predator's eggs, and ultimately its larvae, can be placed near or on the host egg mass. The cover, however, may still represent an obstacle to successful attack. Many wasps only utilize hosts that are in a specific stage of development (Vinson 1976). The cocoon cover could limit information on the status of the host to predators landing on the cocoon, thereby forcing them to waste time or energy cutting a hole in the cover or inserting

their ovipositors into the cocoon to check on host condition. The large number of cocoons which T. ovivora rufopectus sampled without ovipositing suggests that this wasp cannot determine host quality without inserting its ovipositor into the cocoon (Dethier 1947). Indeed, this wasp has indentations along the tip of its ovipositor similar to sensory pits described by other workers (Fulton 1933, Salt 1937, Varley 1941, Fisher 1971) (Fig. 6-4).

In addition, many parasites use chemicals to mark previously searched hosts so further time and energy are not wasted returning to and exploring a nonproductive host (Salt 1937, Price 1970a, Vinson 1972). These chemicals have a number of effects, including the attraction of hyperparasites (DeBach 1944, Price 1970b, Vinson 1975, 1976). I have observed small circles of the hyperparasites of T. ovivora rufopectus stroking the surface of A. aurantia cocoons with their antennae and chewing into the cocoon. I have also found the chewed entrance holes of the hyperparasites and female hyperparasites in approximately 29% of the cocoons that were sampled, but not oviposited into, by this ichneumonid. These observations strongly suggest that this hyperparasite is responding to a marking chemical deposited by T. ovivora rufopectus during oviposition. Attraction to such a chemical may partially explain the relatively high rate of hyperparisitism (59-82%) on this wasp. Increasing the general level of hyperparasites in the habitat by forcing the parasites to mark cocoons would be particularly beneficial if the spider host deposits more than one cocoon in a

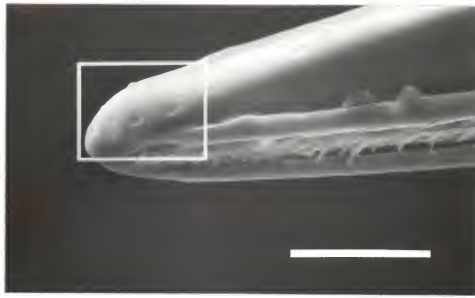


Fig. 6-4. The ovipositor of the ichneumonid Tromatobia ovivora rufopectus showing recessed pits along its length and concentrated at the tip (in the box). These pits are similar to others that have been described as having a sensory function. The scale line equals 20 µm. The ovipositor was plated with 75 Å of gold and observed with secondary electrons.

reproductive season. Indeed, communities of cocoon parasites may be structured by their hyperparasites response to these chemicals (Price 1980).

Successful avoidance of the cocoon cover by initial egg positioning during oviposition, or through the damage done by other predators does not guarantee, per se, that the attacking larvae will have immediate unlimited access to the host egg mass. In many cocoons there is a thick flocculent layer of silk between the egg mass and the cocoon cover which must be crossed. In three field collected A. aurantia cocoons in which oviposition had recently occured, the flocculent silk layers contained the recently hatched eggs of a predator and 20-30 small larvae which appeared dead (no response to gentle prodding). Presumably these larvae died because they ran out of energy or water, but it is conceivable that this silk layer may actually damage the soft cuticle of the larvae much like the trichomes of some plants damage attacking lepidopteran larvae (see Gilbert 1971).

The presence of 8-10 large larvae in the egg masses of the above-mentioned A. aurantia cocoons points out that the flocculent layer is not a complete barrier. However, reducing the absolute number of larvae that can reach the egg mass may be an adequate defense when the egg mass is large. Although the result of the laboratory experiment was not significant, the observed trend further supports the idea of the flocculent silk layer as a barrier to attack.

The flocculent silk layer in the cocoons of M. lemniscata is extremely thin and it seems unlikely that it provides much in the way of a barrier to parasite larvae. However, this spider periodically collapses its orb-webs as they become damaged or dirty, and these collapsed webs are applied to the cocoons on the string. This adds a thick external layer of silk and detritus to the cocoons that may make it more difficult for the eulophid wasp, which is relatively small, to gain access to the cocoon shell for drilling (see Opell 1984). This layer may also work as a further barrier against the mantispid larvae.

Obviously, the various layers of the cocoon may also interact with each other to reduce successful parasite attack. The cocoon of A. aurantia is suspended in the vegetation by a cloud of silk lines which arise from suspension line deltas on the cocoon surface (see Fig. 2-2a). If suspending the cocoon was the only purpose of these lines, the majority of them should arise from the top of the cocoon, with a few on the sides and bottom to provide stability and prevent rotation. However, the greatest number of deltas are found in the middle of the cocoon where the lines emanating from them would contribute little to cocoon support. This is puzzling until the position of the egg mass within the cocoon is considered. The egg mass is closer to the cocoon cover in the upper part of the cocoon because of its shape, and here the average ovipositor can reach it. However, the egg mass is shielded at its top end by a cone of silk and a thick cap of silk (the cup in which the eggs were initially deposited) (see Fig. 2-2b), and the low number of ovipositor drill

holes in the top of the cocoon suggests that these structures are hard to drill through (see Table 6-7). In the bottom third of the cocoon, the egg mass is, on average, further from the cover than the ovipositor can reach. An attack here would result in eggs being deposited in the flocculent silk layer where the hatching larvae have a high probability of becoming entrapped. The number of drill holes is low in this end of the cocoon as well. The middle of the cocoon represents the best fit between ovipositor length and distance to the egg mass without interference from a mechanical barrier, and the number of drill holes is greatest in the the middle of the cocoon's surface (see Table 6-7). However, the distribution of drill holes is identical to the distribution of support line deltas. This suggests that the "suspension" lines are located to interfere with the wasp during oviposition, either by making it difficult to get to the cocoon surface in this area, or by making it difficult to insert the ovipositor maximally, thereby causing eggs to be deposited in the flocculent layer.

Given the relative size and strength of foraging passerine birds, it seems unlikely that the cocoon of A. aurantia provides much resistance to attack. However, many birds dislike coming in contact with spider webs and the suspension system, and consequently A. aurantia cocoons, might be avoided for this reason. Hiding the cocoon might be a more appropriate measure against visually hunting predators such as birds. However, there was no significant difference between those cocoons attacked by birds and those not attacked with regard to how well they were concealed by dead leaves

and other vegetation. The cocoons of M. lemniscata are not attacked by birds at all, even though they are visible in the habitat. This may be for a number of reasons. First, they are extremely small and probably do not give much return for the energy invested in harvesting them. They are also very hard. In addition, they may be covered with old web and prey remains, and appear as detritus to visually hunting predators. Finally, they are hung away from perches on their suspension lines and would be difficult to take except while hovering.

In the preceeding discussion, I have dealt primarily with the cocoon as a barrier to attack once the cocoon has been located by a predator. However, the field evidence suggests that a number of cocoons in the habitat are never found by T. ovivora rufopectus or P. signata. Failure to locate hosts may also explain the low overall percentage of M. lemniscata cocoons attacked by the Tetrastichus wasp. A number of factors may contribute to the inability of a parasite to locate hosts, including the behavior of the host itself. The spatial and temporal aspects of host reproduction, and their effects on successful parasite foraging are considered in Chapter VII.

CHAPTER VII
COCOON SPACING AND THE TIMING OF PRODUCTION AS METHODS TO AVOID EGG AND SPIDERLING PREDATORS

Introduction

Current evidence indicates that parasitoid species do not search randomly, but rather are directed to their hosts through a hierarchy of specific physical and chemical cues which function to reduce and restrict the area and habitats searched and subsequently increase the probability of finding a suitable host (Salt 1935, Flanders 1953, Doutt 1959, Vinson 1976). In addition, behavioral evidence suggests that parasitoids discriminate between areas of high and low host density and allocate greater proportions of their searching time to areas in which host density is high (Waage 1979). This latter behavior has been termed "parasitoid aggregation" or "non-random search" (Hassell and May 1973, 1974, Hassell 1978).

Parasitoid aggregation should cause host mortality to be high in areas where host density is high, while patches of low host density, where the probability of parasitoid attack is low, should represent refuges for the host (May 1978). Although true for some insects (Hassell 1966, McClure 1977, Washburn and Cornell 1979), negative correlations between host number and the level of parasitoid attack (Hassell 1966, Morrison et al. 1980) or lack of any correlation (Dowell 1979, Morrison et al. 1980) are more frequent findings (Morrison and Strong 1980). When a

density-dependent pattern of parasitoid attack is not observed, some factor has usually been suggested as acting to interfere with the parasitoids' search. Suggested factors include tidal inundation of hosts (Stiling and Strong 1982), temperature and humidity (Vinson 1976), heavy rain fall (Stiling and Strong 1982), differential response to hosts at different densities (Hassell and May 1973), insufficient numerical response, dispersal and/ or reduced search efficiency due to mutual interference (Hassell 1971, Hassell and May 1973, 1974), or "pseudo-interference" (Free et al. 1977).

Considerations of host behaviors such as the phenology of host emergence or the timing of host production, and their effects on the temporal and spatial distribution of the host or its reproductive stages have not often been considered as factors affecting parasitoid search, although an understanding of spacing and timing in general are important to our overall understanding of host/ parasite interactions (Murdoch and Oaten 1975, Morrison and Strong 1980). In addition, this predicted relationship has not been tested for any spider and its parasites, although spiders and their cocoons can be heavily attacked (see Eason et al. 1967).

Here, I test the prediction of a positive relationship between host density and the level of parasite attack for the cocoons of the spider Mecynogea lemniscata (Walckanear) (Araneidae) and its primary egg predator, the wasp Tetrastichus sp. (Eulophidae) [near T. banksii Howard; see Hieber (1984)]. I then examine the early and narrow reproductive season of this spider, the timing of cocoon production, the spatial distribution of the cocoons within the

habitat, and the temporal appearance of the cocoons in space as host behaviors that function to reduce egg predator success by making hosts difficult to locate. Finally, I conclude that these behaviors account, in part, for the low rates of parasitism and the observed relationship between host density and the level of egg predator attack.

Materials and Methods

This study was conducted from 1981 to 1984 in mesic, flood-plain woods surrounding Lk. Alice on the campus of the University of Florida, Gainesville, FL. Host density was determined by collecting all the cocoons from areas of known volume. For 1981, the sampling was done in one 800 m^3 plot (10 x 20 x 4 m). In 1982, four 200 m^3 plots (7 x 7 x 4 m) were sampled to determine the variation in host density within the habitat. During the sampling of the 1982 plots, both currently produced cocoons and cocoons from the previous year(s) were collected. In 1983, the sampling was done in one 400 m^3 plot. The sampling height of 4 m was chosen after I observed that less than 5% of the cocoons in the population were deposited above this height.

All the cocoon strings collected each year for the host density determinations were brought into the laboratory and the individual cocoons in each string were cut open and scored for parasite attack (the presence of larvae, pupae, or shed pupal exuviae), or the number of eggs or spiderlings they contained. The position of

parasitized cocoons within a string and the total number of cocoons in each string were also recorded.

The relationship between host density and level of parasitism among sites of high and low host density was determined from the four plots sampled in 1982. For each plot the proportional survival (S/N; number of unparasitized cocoons/ total number of cocoons) was calculated and plotted against the cocoon density (N). The relationship between host density and level of parasitism within a site was determined by dividing the 400 m^3 volume surveyed in 1983 into fifty 8 m^3 sub-volumes. The proportional survival in each of the sub-volumes with cocoons was calculated and plotted against its cocoon density. Density dependence is indicated by a negative slope for such plots.

Developmental rates for the host and wasp were determined by rearing spider eggs and wasp larvae in 2 dram glass vials stoppered with cotton and maintained at 28° C and 70-80% RH (ambient conditions at the study site). The age of the host at the time of attack was determined by rearing the remaining eggs from three cocoons in which developing wasp larvae were found.

Additional collections of cocoons were made in mid-July [during the peak of wasp attack (Hieber 1984)] and late December in 1983, and in early March in 1984 (just before spiderling emergence) to establish if the parasite overwinters in the cocoon as a prepupae, and if so, when it emerges in the spring. Cocoons from these collections were opened in the laboratory and scored for the presence of wasp larvae, shed exuviae and larvae, or shed exuviae

alone. All the larvae from the March collection were held in 2 dram glass vials at 60-75% RH and 26° C until emergence.

The rate of cocoon production, and the temporal and spatial distribution of the hosts were determined in 1983 by mapping the web-sites (X, Y, and Z coordinates) in the 400 m^3 volume and recording the daily production of cocoons. These data, along with the parasite attack data, were used to determine the overall spacing pattern of the hosts, the spatial distribution of the hosts through time [in both cases using a 3-dimensional nearest neighbor approach; Clark and Evans (1954, 1979)], and the location and time of individual parasite attacks.

Results

The level of cocoon parasitism in the habitat remained relatively constant at 7-9% for all three years (Table 7-1). This level is relatively low compared to the 25-75% levels suffered by other spiders (Edgar 1971, Kessler and Fokkinga 1973, Enders 1974, Tolbert 1976, Prakash and Pandian 1978). The cocoons are not distributed evenly in the habitat. There is variation in both their density across the habitat and within a single plot in the habitat, presumably because of the heterogeneous distribution of young trees and shrubs used by this spider for web supports.

Density dependence is indicated by a negative slope in plots of proportional survival (S/N) against density (N). In this study, there were no density-dependent relationships between the levels of cocoon predation and cocoon density, either among sites in the

Table 7-1. Densities of Mecynogea lemniscata cocoons, and the percentages of cocoons attacked by the Tetrastichus sp. wasp for the years 1981 to 1983. In 1981, on 800 m^3 volume was sampled; in 1982, four 200 m^3 volumes; in 1983, one 400 m^3 volume. The experimental volume for 1983 was further divided to determine the relationship between host density and the level of parasitism within a site.

Year	No. Cocoon Strings	Total No. Cocoons	Cocoon Density (m^3)	No. Cocoons Attacked	% Cocoons Attacked
1981	83	290	.362	21	7.24
1982	35	90	.450	6	6.67
	27	72	.360	5	6.94
	27	55	.275	6	10.90
	16	37	.185	1	2.70
1983	38	117	.292	11	9.40
1983 by Subvolume[a]	8	22	2.750	2	9.09
	6	21	2.625	2	9.52
	3	10	1.250	2	20.00
	3	9	1.125	1	11.11
	3	9	1.125	0	0.00
	2	10	1.250	1	10.00
	2	6	.750	1	16.66
	2	6	.750	0	0.00
	2	3	.375	1	33.33
	1	6	.750	0	0.00
	1	5	.625	1	20.00
	1	5	.625	0	0.00
	1	3	.375	0	0.00
	1	1	.125	0	0.00
	1	1	.125	0	0.00
	1	1	.125	0	0.00
	1	1	.125	0	0.00

[a] Of the 50 subvolumes, 33 contained no cocoons at all.

habitat (Fig. 7-1) or within one site (Fig. 7-2). In both cases, there is no correlation at all between the level of host density and parasitism (both $p > 0.05$), implying that some factor in the habitat is interfering with this predator's foraging and reducing its efficiency.

The average spider in 1983 produced a cocoon every 6.4 days (SD = 3.2, n = 73), and produced a string containing 3.1 cocoons (SD = 1.6, n = 38). This is consistent with the average number of cocoons found in strings in 1981 and 1982 (Table 7-2). Although the average number of eggs in each of the sequentially produced cocoons varied, the distribution of eggs among the cocoons showed a similar pattern. In all three years, the first cocoon produced contained the greatest number of eggs. In addition, egg number declined significantly in the second and third cocoons of the string (all $p < 0.05$). The fourth and subsequently produced cocoons in a string all contained approximately the same number of eggs.

The wasp averaged 16 days to develop (1 day in the egg stage; 5 days as larvae; 10 days as pupae), while M. lemniscata eggs averaged 20 days to develop to the spiderling stage (16 days as eggs; 4 days as deutova until molting). The three batches of eggs reared from attacked cocoons took 16, 17, and 19 days, respectively, to develop under identical rearing conditions. This suggests that the wasp is obligated to attack the cocoon within the first few days of its appearance.

Approximately 50-70% of the attacked cocoons collected during December and March contained diapausing prepupae (Table 7-3). Wasps

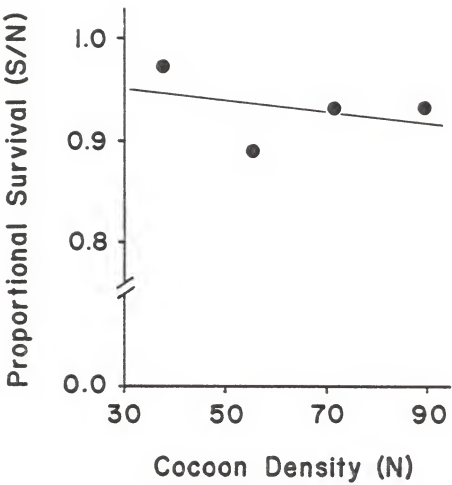


Fig. 7-1. The relationship between proportional survival (S/N) and cocoon density (N) for Mecynogea lemniscata cocoons in four different sites. Proportional survival is not significantly correlated with cocoon density ($Y = -0.0004X + 0.959$; $r = -0.32$, $df = 2$, $p > 0.05$), indicating no density-dependent relationship between predator foraging success and host density.

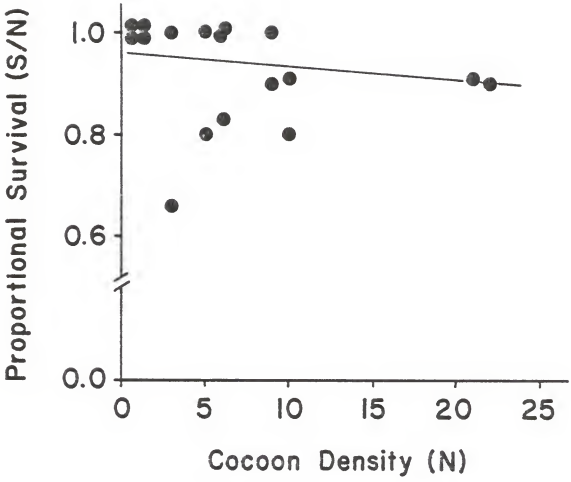


Fig. 7-2. The relationship between proportional survival (S/N) and cocoon density (N) for Mecynogea lemniscata cocoons within one site. Proportional survival is not significantly correlated with cocoon density ($Y = -0.003X + 0.944$; $r = -0.19$, $df = 15$, $p > 0.05$), indicating no density-dependent relationship between parasite foraging success and host density.

Table 7-2. Mean number of Mecynogea lemniscata cocoons per string, and the mean number of eggs in each cocoon in the string for the years 1981-1983. The SD is in parentheses. The sample size (n) is the number below each mean. The number in brackets is the number of times a cocoon in that position in the string was attacked by the Tetrastichus sp. wasp for the sample collected that year.

Year	X No. Cocoons/ String	Average Number of Eggs in Each Cocoon					
		Cocoon #1	Cocoon #2	Cocoon #3	Cocoon #4	Cocoon #5	Cocoon #6
1981	3.5 (1.3) 83	19.5 (6.6) 78 [2]	16.8 (5.5) 69 [4]	14.3 (6.2) 56 [6]	12.8 (4.1) 36 [3]	11.0 (3.7) 9 [3]	9.7 (5.5) 3 [3]
1982	2.5 (1.2) 105	15.8 (6.1) 80 [4]	12.6 (4.6) 53 [9]	10.3 (4.3) 38 [4]	10.2 (4.6) 16 [0]	8.6 (4.4) 5 [0]	8.0 (0.0) 1 [1]
1983	3.1 (1.6) 38	18.5 (5.6) 37 [0]	15.8 (5.3) 25 [2]	12.7 (5.9) 19 [4]	13.4 (5.7) 12 [2]	12.7 (5.4) 7 [2]	15.0 (0.0) 1 [1]

Table 7-3. A comparison of the contents of attacked Mecynogea lemniscata cocoons. Cocoons were collected in the experimental plot in August 1983, and from random locations earlier in July (during the peak in wasp attack), in December, and in March 1984 (two weeks before M. lemniscata emerged from overwintering). The presence of prepupae or exuviae in a cocoon were used as indicators of wasp attack.

Date	No. Cocoon Strings	Total No. Cocoons	No. Cocoons Attacked	No. Cocoons with Prepupae	No. Cocoons with only Exuviae
July	37	125	10 (8.0%)	8 (80.0%)[a]	2 (20.0%)
August	38	117	11 (9.4%)	5 (45.5%)[b]	6 (54.4%)
December	92	357	32 (9.0%)	13 (40.6%)[c]	19 (59.4%)
March	59	254	21 (8.3%)	13 (61.9%)[d]	8 (38.1%)

[a] All 8 cocoons contained only prepupae.

[b] All 5 cocoons contained only prepupae.

[c] Of the 13 cocoons containing prepupae, 6 (18.8%) contained only prepupae, and 7 (21.8%) contained prepupae and shed exuviae.

[d] Of the 13 cocoons containing prepupae, 8 (38.0%) contained only prepupae, and 5 (23.8%) contained prepupae and shed exuviae.

began to emerge in the laboratory from the cocoons collected in March as early as the 4th of May. However, the majority of wasps completed development and emerged between the 24th of May and the 10th of June, 2 to 19 days before the spiders started egg laying in the field.

In 1983, cocoon production started the 12th of June and continued to approximately the 8th of August (Table 7-4). Reproduction was not synchronized, and initially cocoons appeared slowly in the habitat as the early laying spiders started oviposition. For the majority of spiders, the oviposition period ran from approximately the 25th of June to the 25th of July. Early in this period cocoon production increased rapidly with the number of cocoons nearly doubling every 6 days. Cocoon production peaked around the 15th of July and then declined sharply as the majority of the population finished reproduction. Production then continued at a reduced rate until the late starting spiders finished egg laying in early August.

As the number of web-sites with cocoons increased over the season, their distributional pattern changed from one significantly more dispersed than random early in the season (15-21 June), to random (27 June), to a loosely clumped distribution where it remained (3 July to the end of the season) (Table 7-4). The distribution of web-sites with cocoons in the appropriate stage for attack (1-5 days old) showed a similar pattern of change (Table 7-4). Early in the season the distribution of sites with cocoons of this age changed from overdispersed (21 June), to random (27 June),

Table 7-4. The number and distribution in space and time of all Mecynogea lemniscata web-sites with cocoons, and of sites with cocoons of the proper age (1-5 days) for attack, in the experimental plot for 1983.

	Date										
	June			July					August		
	15	21	27	3	9	15	21	27	2	8	14
No. web-sites with Cocoons	2	7	21	34	34	34	35	35	35	35	35
Average No. Cocoons/ web-site	1.0	1.1	1.3	1.6	2.4	2.9	3.0	3.2	3.2	3.2	3.2
Total No. Cocoons for all Web-sites	2	8	28	56	80	99	106	111	112	113	114
No. Web-sites with Cocoons 1-5 Days Old	2	6	14	22	23	12	6	5	1	1	0
% Web-sites with Cocoons 1-5 Days Old	100%	85%	67%	64%	66%	35%	17%	14%	3%	3%	0%

"R" for all Web-sites[a]	2.51[b]	1.60*	0.99	0.77*	0.80*	0.79*	0.77*	0.77*	0.77*	0.77*	0.77*
"R" for Web-sites with Cocoons 1-5 Days Old[a]	2.51[b]	1.43*	1.09	0.83*	0.80*	1.13	0.74	0.41*	---	---	---

[a] The "R" values (a measure of dispersion), and their departures from random were calculated using the procedures outlined in Clark and Evans (1954). R values run from R = 0 indicating maximum aggregation, to R = 1 indicating a random distribution, to R = 2.15 indicating a perfectly uniform distribution. The stared (*) R values indicate a pattern of web-site distribution significantly different from random ($p < 0.01$).

[b] The R values for June 15th are beyond the scale because there were only two web-sites at this time. Their distribution cannot be tested for significant departure from random for this reason as well.

to loosely clumped (3 July). In mid-July (9-21 July) the distribution returned to random as cocoon production declined. Late in the season (27 July), as cocoon production drew to a close, the distribution of web-sites with cocoons 1-5 days old became relatively clumped again.

There were 11 cocoons attacked in 10 different strings by the Tetrastichus wasp in the experimental plot in 1983. These attacks occured between the 6th of July and the 8th of August, with the majority (9 of 11) occuring between the 10th and 23rd of July. Attacks can occur earlier in the year (Hieber 1984). Assuming that overwintering wasps attack cocoons soon after emerging in mid-June, the peak in attack represents the emergence of the second generation of wasps (16 day developmental period; 32 days later) from cocoons attacked in late June-early July.

The concentration of wasp attacks coincided with the end of the peak in cocoon production. Just prior to this period, the ratio of web-sites with cocoons 1-5 days old to all sites with cocoons was at its highest (66%) for the season (see Table 7-4). Over the approximate 15 day period of heaviest wasp attack, however, this ratio dropped to 14% as cocoon production slowed down. At the time of the first attack, the average spider had already produced 58.4% (SD = 22.5%, n = 27) of its 3.1 cocoons. This resulted in the wasp attacks being concentrated primarily on the third cocoon in a string. This pattern is similar for 1981 and 1982 as well (Table 7-2).

Discussion

Explanations of parasitoid foraging suggest they locate hosts through a series of steps mediated by one or more physical or chemical cues. Such models have led to the prediction of density-dependent parasite mortality of the host. Hosts should be under heavy selection for behaviors which reduce or eliminate the quality or number of useable cues available to the host to reduce the probability of its success. For the Tetrastichus wasp, which emerges from cocoons in the host habitat (the woods), a successful search involves locating a string of M. lemniscata cocoons and selecting a cocoon in the proper stage for attack. The low overall levels of parasitism (7-9%) by this wasp in comparison with the levels of parasitism demonstrated by other wasps using cocoons (25-75%), and the lack of the predicted relationship between cocoon density and the level of parasitism suggest that something is interferring with this search process.

Mecynogea lemniscata (Walckenaer) (Araneidae) is the first orb-weaver to emerge in the spring and its reproductive period is shifted to the early summer, far earlier than the other orb-weavers using the woodland habitat. Consequently, M. lemniscata starts egg laying at a time when few other spiders are producing cocoons. This limits the parasites in utilizing other spider hosts to build up their numbers during the early appearance of M. lemniscata cocoons. In addition, M. lemniscata is reproductively active for a 40 day period. This short time interval limits the number of wasp

generations to one or two, preventing a large build-up of predators. The slow initial appearance of cocoons due to the asynchrony of the hosts' reproduction further acts to keep predator numbers down by limiting the number of cocoons initially available to the wasps emerging from overwintering.

More importantly, the rapid rate of cocoon production (every 6 days) in relation to wasp generation time (every 16 days) allows the spiders to produce 1-2 cocoons with high numbers of eggs prior to the emergence of the first generation of wasps in late June-early July. In addition, the number of eggs in the cocoons drops significantly by the third cocoon. Thus, during the peak in attack in mid-July, the majority of cocoons available to the wasps contain less eggs (and less energy) than those produced earlier in the season (see Table 7-2). Overwintering wasps result from cocoons attacked during this peak period, and the reduction in egg number (and energy) may act to reduce the numbers of wasps which emerge the following year.

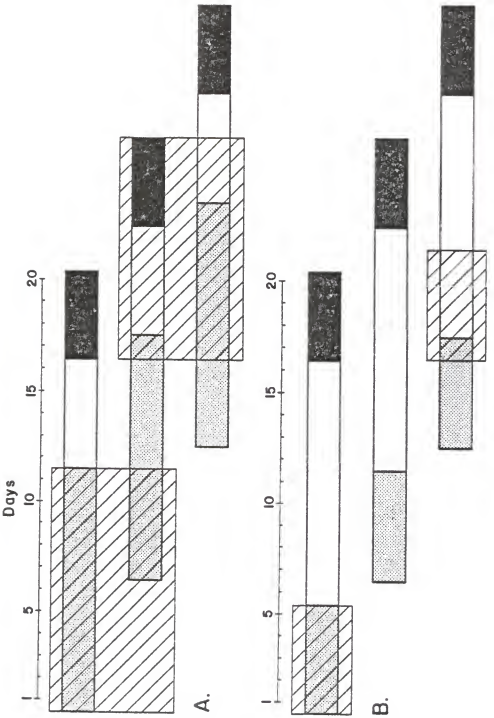
Many parasites are restricted in their attack to a specific time in the hosts' developmental sequence (Vinson 1976). The eggs of M. lemniscata take 16 days to develop to the deutoval stage. The larvae of the wasp take 5 days to develop before pupation. If there is no specific period of time during which attack must occur, the wasp can initiate an attack any time during the first 11 days of host egg appearance to have enough time for development (assuming that the larvae cannot use deutova as food). When such a timing scheme is plotted out for a string of three cocoons, each 6

days apart in age, there are always two cocoons on the string in the proper age for attack (Fig. 7-3a). In addition, one or two other cocoons on the same string are available for attack when the wasp's progeny emerge 16 days later (mating takes place on the outside of the cocoon).

The rearing data suggests, however, that the time period for attack is less than this 11-day period. If a more conservative 5-day period is used as the limit for successful parasite attack, a different picture emerges (Fig. 7-3b). With cocoons produced every six days, there is only one cocoon in the string at any given time in the proper condition for attack. In addition, the timing of cocoon production insures that the emerging progeny barely overlap with one cocoon instead of two. The average string contains only three cocoons, and if the second or third cocoon is attacked, there are no cocoons available for emerging progeny. Thus, the interaction between cocoon production and egg development forces the initally attacking wasp, or its subsequent progeny, to locate other web-sites with strings containing useable cocoons. The low number of multiply-attacked cocoon strings (3.14% of 286 for 1981-1983) supports the hypothesis that timing of cocoon production is a barrier limiting individual parasite success.

In general, web-sites, and thus host cocoons, are slightly clumped in their distribution (Table 7-4). Spiders which utilize sites that are spatially isolated from other web-sites or clumps of sites may therefore have an advantage in avoiding parasites. Although the distance between web-sites may play a role early in the

Fig. 7-3. The number of Mecynogea lemniscata cocoons in a three-cocoon string available to a Tetrastichus wasp or her emerging progeny assuming an 11-day period for attack (A), or a more conservative 5-day period (B). The cocoons in each string are represented by individual bars. In both cases the cocoons are produced every 6 days. The stippled area of each bar represents the period of time (11 or 5 days) during which attack can occur; the stippled and open areas together represent the total 16 days the host is in the egg stage; the solid areas represent the 4 day deutova stage after eclosion. The first cross-hatched box indicates the number of cocoons that can be initially attacked by the wasp. The second box indicates the possible cocoons on the same string that can be attacked by emerging progeny.


Days
1
5
10
15
20
A.
B.

season when they are dispersed and have few cocoons, web-site spacing has little or no effect on the probability of being parasitized. Indeed, many of the cocoon strings attacked in the experimental plot occured at spatially isolated sites (see Figure 7-4).

However, the change through time of the spatial distribution of web-sites with cocoons 1-5 days old may act to reduce the probability of a parasite successfully locating a useable cocoon. The majority of wasp attacks occured between the 10th and the 23rd of July. Just prior to this period (July 3-9), the percentage of sites with useable cocoons was at the highest level for the season (see Table 7-4). Sites with useable cocoons were also slightly clumped in their distribution among all web-sites, which were also slightly clumped. By the 15th of July, the reproductive pulse started to taper off and the number of sites with useable cocoons began to decline. More importantly, during this time period the distribution of sites with cocoons 1-5 days old became random compared to the slightly clumped distribution of all web-sites (see Table 7-4). Many parasites locate their hosts through the use of long-range chemical cues (Vinson 1975, 1976) and then use short-range cues to determine the location and quality of the host (Laing 1937, 1938, Eason et al. 1967, Vinson 1976). Since long-range cues rarely provide information about the quality of the host, the "switch" to a random distribution of hosts would lower the probability that a parasite will find a cocoon since a response to cues from an area of high cocoon density guarantees only a random

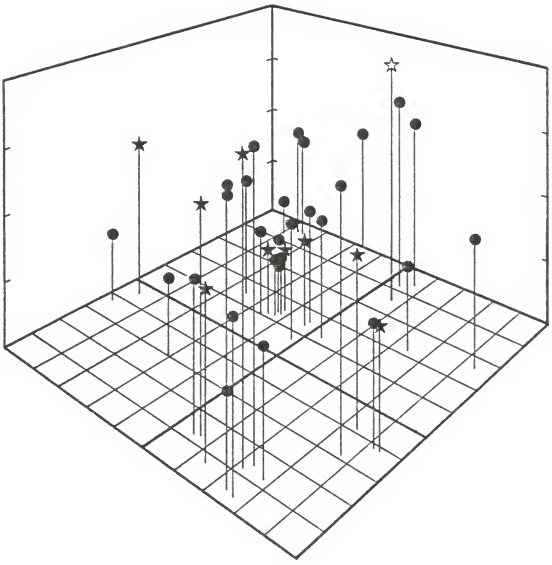


Fig. 7-4. The spatial distribution of all the Mecynogea lemniscata web-sites with cocoons in the 4 x 4 x 10 m experimental plot for 1983. The distribution of web-sites is slightly clumped ("R" = 0.77; see Table 7-4). Web-sites containing strings with attacked cocoons are indicated with stars. The site with the open star had two cocoons attacked in the string. The location of web-sites with attacked cocoons is unrelated to their distance to other cocoons or clumps of cocoons.

chance of a site with a useable cocoon. The random distribution of sites with 1-5 day old cocoons remains until late July when sites with useable cocoons again show a clumped distribution (see Table 7-4). However, by this time sites with cocoons 1-5 days old are rare, and the probability of locating one against the background of older sites with nonuseable cocoons is low.

The low probability of locating a cocoon due to these spatial and temporal effects may be further reduced if visual cues are used by this wasp for host location (Laing 1937). Approximately 50-64% of the cocoon strings collected in each of the four plots in 1982 were from the previous year(s). These strings were still hanging in position, and presumably represent nonproductive sites which would have to be examined at a cost in energy and time.

The preceeding discussion suggests that the low overall levels of parasitism in this system can be explained by the short reproductive season, which limits the number of wasp generations, and the timing of egg development and cocoon production, which limits the number of cocoons attacked in any one string. Both have the effect of forcing wasps to look for new strings of cocoons. It also suggests that the lack of a density-dependent relationship can be explained by the interaction between the short reproductive season, the rapid rate of cocoon production, and the limited time period for successful cocoon attack. These factors force wasps to locate a constantly decreasing number of randomly distributed useable cocoons among a rapidly increasing number of web-sites with cocoons too old for successful attack.

Obviously, there are other factors which may also account for the observed levels of parasitism and the lack of a density-dependent relationship. It is possible that this Tetrastichus species has other hosts, and that the eggs of M. lemniscata represent either a secondary host, or one of several alternatives used when they are accidentally discovered while searching for the primary host. Indeed, wasps in this genus can be quite catholic in the host preferences (Burks 1979). However, the presence of prepupae in cocoons collected late in the year, and the close timing of wasp emergence with the onset of cocoon production strongly suggest that the eggs of M. lemniscata represent a primary host for this wasp. The observed patterns may also be partially related to mutual interference (Hassell 1971) in response to "trail-marking" substances (Price 1970a), or simply to variation in the "toughness", and thus ease of entry, of the available cocoons in the habitat (see Chapter VI).

The above discussion implies that the observed pattern of reproductive phenology and rates of cocoon production are adaptations which have evolved in response to parasite pressure. Certainly the 7-9% level of parasitism represents sufficient evolutionary pressure to select for such behaviors. The parasite and the host also appear to be closely linked, as demonstrated by the relatively constant levels of host density and parasitism, the timing of parasite emergence with host emergence, and the timing of the wasp attack with the peak availability of cocoons. In addition, the rate of cocoon production in Florida (6.4 days, SD = 3.2, n =

73) is not significantly different from the rates Eberhard (1979) found for M. lemniscata in Washington, D.C. (5.6 days, SD = 2.8, n = 15) and Central America (6.3 days, SD = 2.1, n = 20). Since climate and the abundance of food vary at these sites, these factors are probably not responsible for the observed timing of cocoon production. All of these facts support parasite avoidance as the selective pressure setting reproductive rates. However, the rate of egg production could also represent some physiological limit independent of food intake, or selection for rapid reproduction in response to high levels of maternal predation. Adult female M. lemniscata are preyed upon heavily in June by mud-daubing wasps (Hieber, unpub.) and in July by kleptoparasitic Argyrodes spp. (Araneae: Theridiidae) in the webs (see also Trail 1980, Wise 1982).

The phenology of reproduction may also be partially accounted for by other factors. The shift to an early spring appearance has been suggested as a way of taking advantage of abundant insect prey in the habitat, while avoiding competition from other orb-weavers which use the woodland habitat later in the season (Anderson 1978).

CHAPTER VIII
GENERAL DISCUSSION AND CONCLUSIONS

General Discussion

Spider cocoons range in complexity from a few threads surrounding the egg mass (e.g., the Pholcidae) to large complex structures composed of many layers (e.g., the Araneidae) (McCook 1890, Scheffer 1905, Kaston 1948, Turnbull 1973). Cocoons are believed to protect the eggs or spiderlings by reducing the detrimental effects of a number of biotic and abiotic factors (Turnbull 1973, Foelix 1982, Austin, In press). However, with few exceptions, none of the roles attributed to cocoons have been tested.

I examined the effects of cocoon architecture on two abiotic factors, temperature extremes (Chapter III) and dessication (Chapter IV), and on the biotic problems of fungal attack (Chapter V) and predator attack (Chapter VI). Chapter VII is closely linked with Chapter VI and examines the temporal and spatial strategies that spiders have evolved to reduce the initial probability of a predator locating a cocoon. The primary technique I used was to modify the cocoons and relate these modifications to changes in egg hatching success and spiderling survival. The direct connection between the function of the cocoon or component parts and measures of fitness avoids many of the problems found in other ecological or

behavioral studies (e.g., foraging behavior). In the latter, a number of initial assumptions, often unrealistic, must be made concerning what is being maximized and how it relates to fitness.

Many authors have suggested that cocoons, and in particular the flocculent silk layers often found within cocoons, function as insulation and protects the eggs and spiderlings from extremes of temperature (McCook 1890, Kaston 1948, Turnbull 1973, Gertsch 1979). Chapter III supports this view, and indicates that the protection provided may be directed primarily at controlling short-term radiation loads (i.e., "sunflecks"). The limited level of protection offered by the cocoon is due to the cocoon cover, which creates an insulating layer of dead, and, to a greater extent, the size of the egg or spiderling mass which provides thermal inertia. The flocculent silk layer has no role in the insulation of the cocoon.

The size of the cocoon and the spiderling mass must be considered before these results are extended to all cocoons. The cocoon and egg mass of A. aurantia are among the largest found (Kaston 1948, Foelix 1982). As such, the level of protection against short-term thermal loads provided by this cocoon and its egg or spiderling mass is probably close to some maximum value. Cocoons without covers which cannot produce a layer of dead air (Kaufman et al. 1982), or cocoons with smaller egg masses would show proportionately smaller effects in attenuating thermal extremes. The position of the cocoon in the habitat probably plays a more effective role in controlling thermal extremes for most spiders.

Given the time that the eggs, and particularly the spiderlings, of many species spend in the cocoon (Anderson 1978), it seems likely that this structure functions to control water loss. This is the most commonly held assumption about the function of cocoons (e.g., Foelix 1982). However, previous work relating the cocoon to dessication control has been contradictory. Schaefer (1976) demonstrated that the parchment-like cocoons of the linyphiid Floronia bucculenta increased the survival time of post-diapause eggs. However, Austin and Anderson (1978) could detect no role in desiccation resistance for the flocculent silk cocoon of the araneid Nephila edulis.

The results of Chapter IV demonstrate that the cocoon of Mecynogea lemniscata has no effect on hatching or molting success but does have a significant effect on spiderling survival. In contrast, the cocoon of Argiope aurantia has no apparent effect on hatching success, molting success, or spiderling survival. These results indicate that the level of protection provided by cocoons to eggs or spiderlings is related to the length of time these developmental stages spend in the cocoon. The eggs Schaefer (1976) used in his study were post-diapause eggs approximately 180 days old (F. bucculenta overwinters in the egg stage). These eggs are apparently not very resistant to desiccation, and the cocoon may provide the protection necessary for the eggs to make it through this long period. In comparison, the eggs of Nephila clavipes (Christenson and Wenzl 1980), M. lemniscata, and A. aurantia all hatch in approximately 16 to 30 days. This may be too short to

demonstrate a protective function provided by the cocoon. The significant effect of the cocoon on the survival of M. lemniscata spiderlings appears to be related to the exceedingly long time that they spend in the cocoon overwintering (2-3 months longer than orb-weavers). Overall, the results of this study and those of Schaefer (1976) and Austin and Anderson (1978) show that covered cocoons should be found in species that spend long periods of time as eggs or spiderlings in the cocoon in developmental diapause or overwintering, or where the habitat is extremly xeric for all or part of the year.

The results also emphasize that physiological or morphological differences in the abilities of deutova and spiderlings to limit water loss may also be operating in conjunction with, or in place of, the cocoon. With no cocoons present, the deutova of M. lemniscata molted successfully at much lower humidities than those of A. aurantia. The survival rate for M. lemniscata spiderlings without cocoons was also higher than those of A. aurantia at lower humidities. Both of these results suggest that the deutova and spiderlings of M. lemniscata are better able to handle desiccation.

Finally, the results suggest that the above mentioned differences might be part of a behavioral solution for controlling water loss. The limited survival of A. aurantia spiderlings with a cocoon at low humidities points out that other considerations, such as the RH humidity at the oviposition site, are more important for this spider. Indeed, Levi (1968) notes that of the Argiope species

in Florida, A. aurantia prefers moister habitats and is one of the first Argiopes to disappear during droughts.

Morphological differences between the eggs of spiders, or differences in the sizes of the egg masses also affect hatching success. At low humidities the egg mass of A. aurantia (which is 70 times larger than the egg mass of M. lemniscata) has a significant advantage in hatching success when naked egg masses of the two species are compared. This advantage disappears when the egg masses of A. aurantia are reduced to the same size as those of M. lemniscata. Here, the egg masses of M. lemnimcata demonstrate significantly greater hatching success, and these differences appear to be related to a significantly denser layer of spherical granules on the surface of the M. lemniscata eggs.

These morphological and size related advantages are exciting for a number of reasons. All of the spider eggs so far observed have a layer of mucoid granules on their chorions (Austin and Anderson 1978, Grim and Slobodchikof 1978, 1980, Humphreys 1983), and this layer has been previously suggested to function as a barrier to water loss (Austin and Anderson 1978). The results of this study provide the first evidence supporting this hypothesis.

Both the density of the spheres on the chorion and the size of the egg mass function to reduce water loss, presumably by reducing the area available for evaporation. This suggests that small egg masses with dense sphere coatings and large egg masses with less dense coatings may represent solutions for dessication control. I looked at the relationship of sphere density to clutch size. Since

clutch size data are not available for the data of Grim and Slobodchikoff (1980, 1982), I used clutch size data for conspecifics of the same relative body size from the literature (see Table 8-1).

The relationship between sphere density and clutch size is shown in Fig. 8-1. A Spearman rank correlation, which is conservative in its treatment of the tail values, is not significant ($r = -0.367$, $p = 0.035$), falling just short of the 0.05 level of acceptance. However, the data incorporate a substantial amount of variation, and the analysis therefore represents a conservative test of the relationship. The fact that a relationship emerges and hovers around significance suggests that the relationship is real and would show significance if species-level rather than congeneric-level data were used.

Finally, the advantage of a large clutch size in controlling temperature extremes and water balance points out that selection for clutch size may be driven by abiotic factors. This is in direct contrast to much of the vertebrate literature that lists primarily biotic factors (e.g., food supply, parental efficiency, or predators) as the major selective forces working on clutch size (e.g., Lack 1954, 1966, 1968).

The results presented in Chapter V indicate that the cocoon, and in particular its suspension system, function to prevent the eggs or spiderlings from drowning (see also Schaefer 1976, Reichert 1981). A strong suspension system appears to be particularly important for small cocoons that have a high probability of being worked into the soil and consequently drowned due to their constant

Table 8-1. The mean sphere density (± 1 SD), and median clutch size for individual spiders from different families. The sphere density values are from Gim and Slobodchikoff (1982). The clutch size data has been taken from the literature. The numbers in brackets are the range of clutch size values used to calculate the median clutch size.

Family	Genus and species	Sphere Density ($spheres/100\ \mu m^2$)	Median Clutch Size
Theraphosidae	Dugiesiella sp.	10.00 (5.30)	812[a]
Theridiidae	Lactrodectus hesperus Chamberlin and Ivie	24.69 (5.40)	196[b]
	Steadota grandis complex Banks	54.38 (18.10)	62 [37-95][c]
	Argyrodes baboquivari Exline and Levi	48.13 (11.80)	32 [15-49][d]
	Theridion sp.	97.50 (27.35)	69 [19-442][e]
Araneidae	Araneus normandii Thurell	4.84 (1.90)	700 [284-887][f]
	Argiope aurantia Lucas	17.00 (4.20)	978 [350-2000][g]
	Mecynogea lemniscata (Walckenaer)	21.60 (5.50)	14 [8-30][g]
Agelenidae	Barronopsis floridensis (Roth)	184.38 (24.20)	130[h]
Lycosidae	Lycosa santrita Chamberlin and Ivie	126.25 (30.30)	207 [32-600][j]
	Lycosa sp.	35.00 (9.86)	207 [32-600][j]
	Pardosa makenziana (Keyserling)	103.13 (27.20)	41 [12-106][k]
	Pardosa yavapa Chamberlin	211.20 (37.70)	41 [12-106][k]
Clubionidae	Castineira luctifiera Petrunkevitch	89.38 (14.70)	14[m]
Philodromidae	Philodromus sp.	78.75 (20.60)	30 [7-104][n]
Salticidae	Phiddipus octopuctatus McCook	80.63 (14.60)	90 [43-166][p]

[a] Gertsch (1979)

[b] Kaston (1970)

[c] from Steatoda borealis (Kaston 1948)

[d] from Argyrodes trigona (Kaston 1948)

[e] from Theridion tepidariorum, T. differens, T. murarium, T. spirale, T. frondeum, T. albidum, T. unimaculatum, T. punctosparsum, T. redimitum (Kaston 1948)

[f] from Araneus diadematus, A. cornutus, A. sericatus, A. marmoreus, A. trifolium, A. pima, A. gemmoides (Kaston 1948)

[g] This study

[h] from Agelenopsis pen[n]sylvanica, A. naevia (Kaston 1948)

[j] from Lycosa carolinensis, L. aspersa, L. rabida, L. punctulata, L. avida, L. helluo, L. modesta, L. gulosa, L. frondicola, L. avara (Kaston 1948)

[k] from Pardosa distincta, P. moesta, P. milvina, P. saxatalia, P. floridana, P. mochia, P. lapidiana, P. xerampelina (Kaston 1948)

[m] Reiskind (1969)

[n] from Philodromus praelustris, P. pernix, P. imbecillus, P. rufus, P. aureolus (Kaston 1948)

[p] from Phiddipus audax, P. purpuratus, P. clarus, P. princeps, P. whitmanni, P. insignarius (Kaston 1948)

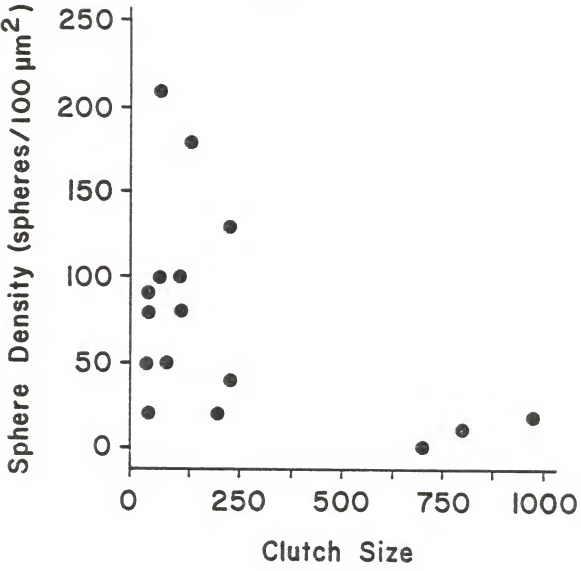


Fig. 8_1. The relationship between mean sphere density (spheres/ 100 μm^2) and clutch size for individual spiders from different families.

exposure to soil moisture. This is apparently not a problem with large cocoons which are not moved down into the soil and therefore dry out between rains.

The suspension systems and covers also retard water entry, but the relation between this function and the prevention of fungal attack is less clear. The covers of M. lemniscata and A. aurantia cocoons do not control fungal attack in the egg stage. However, the flocculent silk layers in both of these cocoons are difficult to wet, and this layer was left intact during the field experiments. This could account for the lack of any effect from cover damage. Although the cover of M. lemniscata cocoons controlled fungal attack in the spiderling stage, the cover of A. aurantia cocoons did not. The differences in the incidence of fungal attack in the spiderling stage may also be related to the flocculent layer, to the time spent in the cocoon, and cocoon size. It is also possible that the observed differences in egg and spiderling survival between these two cocoons have nothing to do with the size or presence of various layers, but rather with the chemical composition of the structure itself. Some spiders manufacture anti-fungal materials which are applied to their webs (Schildknecht et al. 1972). Such materials may also be used to protect cocoons.

One obvious function of cocoons is to protect them from mechanical shock or damage (Opell 1984). In many of my fungal and predator attack experiments, the cocoons of M. lemniscata tied to vegetation, and those of M. lemniscata and A. aurantia placed on the ground were dented or partially collapsed by the falling rain.

For some, the impact of the rain was enough to crush the cocoons and kill the contents. This suggests that the cover and suspension system of many cocoons function to cushion the contents by deflecting falling rain and absorbing its shock, or to keep the cocoons off non-yielding surfaces where the force of the rain may be concentrated. Such a protective role also explains the increase in fungal attack that N. clavipes cocoons suffered when their protective leaf canopies were removed (Christenson and Wenzl 1980). With no canopy above the cocoon, rain would not be deflected from the cocoon nor would its velocity be diminished. In this condition, water would be driven deep into the cocoon carrying fungal spores with it. In contrast, the cocoons of M. lemniscata and A. aurantia, even with some cover damage, might still be able to deflect much of the rain striking the cocoon or reduce its velocity.

The importance of the leaf canopy to N. clavipes illustrates the importance in selecting specific sites for oviposition. Many spiders locate their cocoons in crevices, under bark, or in the leaf litter (McCook 1890, Kaston 1948, Turnbull 1973, Gertsch 1979), presumably to avoid abiotic problems. If such sites are limiting, covered cocoons, by creating protective microclimates, would allow spiders to use a wider variety of potential habitats and web-sites.

The large and diverse number of predators and parasites attacking spider cocoons, and the wide range in complexity of cocoon architecture have led many to speculate that the primary purpose of cocoons is to protect the eggs and spiderlings from attack (Austin and Anderson 1978, Christenson and Wenzl 1980, Robinson 1980). More

recently, Austin (In press) has considered cocoon architecture and its relationship to predators and parasites. He suggests that the cocoons of spiders function against two groups: 1) oppurtunistic scavenging predators (generalists), such as ants or beetles, and 2) groups such as ichneumonid wasps, mantispids, and chloropid flies (specialists) which are highly adapted for preying exclusively on spider eggs. He further suggests that a coevolutionary "arms race" (e.g., Krebs and Davies 1979) between spiders and the specialized parasites and predators is responsible for the wide range of structural diversity apparent among spider cocoons today. As such, Austin's paper forms a convenient outline for discussing the results of Chapter VI.

Predation pressure from generalists should show up as cocoon adaptations which are generally distributed among a wide variety of spiders, since generalist predators are distributed across habitats. Austin (In press) suggests that the cocoon cover and maternal guarding are adaptations against generalists, and should provide high levels of protection. The results support this view. Approximately 23% of the covers of the 185 A. aurantia cocoons collected in 1982 were damaged by unknown predators (Table 6-4). In many of these cocoons there was no damage to the egg or spiderling mass, suggesting that the cover turned the attack away. Enders (1974) mentioned a generalist predator, a Chaulignatus beetle, that attacks the cocoons of A. aurantia. He described damage similar to my observations. Other structures common to many cocoons may also work against generalist predators. Many cocoons have suspension

systems that isolate the cocoon from the substrate and effectively reduce its accessibility to general pedestrian predators. Both M. lemniscata and A. aurantia cocoons suffered significant increases in egg and spiderling mortality when the cocoons contacted the vegetation or fell to the ground and became accessible to arboreal predators (ants) and terrestrial predators (ants, rodents, and possibly birds). Those cocoons which remained in place were almost never attacked by these groups (excepting birds; see Tolbert 1976), underscoring the effective barriers that suspension systems make against these predators.

If coevolution between spiders and their specialized egg predators is responsible for the diversity of cocoon architecture (Austin, In press), cocoons should demonstrate specific defenses against these specialized attackers which reflect the manner in which they attempt to introduce themselves or their eggs into the cocoon. Overall, the results presented in Chapter VI demonstrate that a dense cover is an adaptation to control actively searching larval forms. The most striking example was the control exerted by the cover of M. lemniscata cocoons against the mantispid egg specialist Mantispa viridis. This parasite is an obligate cocoon attacker (Redborg and MacLeod, In press), the larvae actively locating and burrowing into cocoons. Parasitization rates rose dramatically from 1-4% to approximately 63% when the cover of this cocoon was damaged (see Table 6-2), suggesting that the larvae of this species have no trouble in locating cocoons (Hieber 1984), but are almost completely stopped by the cocoon cover. The large

numbers of unsuccessful fly attacks on A. aurantia cocoons, and the apparent preference of Pseudogaurax signata for cocoons with covers damaged by other predators provide further support for the idea of covers as specialized layers to control certain predators.

Dense covers may also be effective against wasps with short ovipositors. The Tetrastichus wasp probably attacks the cocoons of M. lemniscata by ovipositing into the top layer (Austin, In press); the first instar larvae then burrowing through the cocoon wall to attack the eggs. Unless the eggs are initially deposited through the extremely hard cover, the larvae probably have a hard time penetrating the cocoon (see also Kaston and Jenks 1937). The old web deposited on the cocoon string may act to hide the dense cocoon cover and fool the wasps into ovipositing into what appears to be the outer layer of the cocoon, or keep them elevated off of the true cocoon surface so that their ovipositors cannot completely penetrate the outer cover (Opell 1984).

Although the covers of cocoons may force some wasps to waste time and energy drilling through the cocoon to determine host quality or to mark previously visited cocoons (which provides cues for hyperparasites), cocoon covers appear to be only secondarily related to controlling wasps with long ovipositors (e.g., the ichneumonids). However, the distance of the egg mass from the cocoon cover and the layer of flocculent silk between the cover and the egg mass appear to be adaptations directly related to controlling such wasps (see also Austin, In press). The separation makes it difficult for wasps to deposit eggs directly on the host

egg mass, and the silk layer entraps emerging larvae as they move toward the host eggs. Although not 100% perfect, the flocculent silk layer substantially lowers the number of larvae which make it to the host egg mass and is increasingly effective when the egg mass is large. Under the best conditions, the principle predator of A. aurantia cocoons, Tromatobia ovivora rufopectus, destroys only 90% of the eggs in a cocoon. In contrast, the predators of M. lemniscata cocoons, which have small egg masses and a thin flocculent silk layer, always destroy all of the eggs in an attack. Many other araneids (e.g., members of the genera Araneus, Gastercantha, Neoscona, and Nephila) utilize flocculent cocoons without covers. These spiders also have relatively large egg masses, suggesting that the combination of this layer and a large egg mass may be a part of a set of adaptations for controlling wasps. Austin (In press) points out that many scelionid wasps cannot parasitize more than about 35% of some large host egg masses because their ovipositors cannot reach further into the mass than the upper two layers of eggs.

Chapter VI also demonstrates the integrated nature of the various layers in defending the cocoon. For example, the suspension system of A. aurantia cocoons fuctions to protect the eggs and spiderlings from predators by keeping the cocoon away from contact with the vegetation and off of the ground. Moreover, the suspension lines on the cocoon are distributed in the areas of best fit between the ovipositor of the ichneumionid predator and the distance to the egg mass, presumably to interfer with oviposition.

As a family, the orb-weaving spiders (Araneidae) are attacked by a wide variety of specialized predators from a number of the major insect groups (Eason et al. 1967, Askew 1971, Austin, In press). The results of Chapter VI study suggest that a covered cocoon with a thick flocculent layer (e.g., the cocoon of A. aurantia) may be the best combination for discouraging the widest variety of predators. However, many genera of araneids use flocculent cocoons which small wasps and flies can apparently enter with relatively little hindrance (see e.g., Muma and Stone 1971). In addition, many spiders position their cocoons in what appear to be locations that are higly accesible or easy to locate. This suggests that many spiders are using methods that reduce the numbers of predators and parasites that initially locate the cocoon.

One method of reducing the number of predators that will potentially locate a cocoon is to limit the availability of the cocoons in time (Chapter VII). This could involve shifts in the oviposition season to times when parasites are less abundant, or a shortening of the reproductive season. Mecynogea lemniscata reproduces early in the summer at a time when few other spiders are reproductive. Reproduction at this time could reduce the overall numbers of parasites present in the habitat, as well as limit them from building up large numbers because of the lack of alternative hosts. Enders (1974) has demonstrated the positive effects of such a temporal shift in the reproductive period for Argiope trifasciata Forskal (Araneidae). The reproductive season of M. lemniscata is also relatively short, subsequently limiting the number of parasite

generations that can occur in a given reproductive season. This could further act to keep the overall number of parasites available for attack low.

Escape can occur within a much shorter time scale if the predator or parasite is limited to attacking the host within a narrow developmental period. Both the eggs of A. aurantia and M. lemniscata appear to present such limitations. In addition, the timing of M. lemniscata cocoon production is such that only one cocoon on a given string is available to an attacking wasp or her emerging progeny. The interaction between the developmental constraints and the timing of cocoon production for M. lemniscata leads to two important outcomes. First, it limits the number of cocoons at any one site which can be attacked by a wasp. This forces the wasp to move off and look for another site. Second, it results in a spatially variable pattern of cocoon distribution over time. During the peak in wasp attack, this interaction results in a random spatial distribution of useable cocoons that the wasps must locate against a constantly increasing background of older non-attackable cocoons.

The suspension systems and cocoons of M. lemniscata and A. aurantia function in controlling the access to the cocoon of a number of generalized and specialized predators (Chapter VI). These results and the limited control that the cocoon of A. aurantia exerts on the abiotic factors examined (Chapters III, IV, and V) suggest that the main function of most spider cocoons and their associated structures is to control parasite and predator attacks.

The results of Chapter VI also support the idea that much of the observed variation in cocoon architecture is related to limiting such attacks (Austin, In press). Does this imply that cocoon architecture is the result of coevolution to avoid predator and parasite attacks? Intuitively this proposal seems logical. Many of the cocoon layers function to limit access to specific predators. In addition, whole families of predators (e.g., the mantispidae) have specialized on spider eggs. Since the Neuroptera in general are a relatively old group, this family level specialization suggests that some relationships between spiders and their predators and parasites have existed for long periods of time.

Coevolution in its strictest definition is at least a three step evolutionary sequence involving two interacting gene pools in which the traits of one population change in response to the traits of another, followed by changes in the first population in response to the changes of the second (Jantzen 1980). For example, a spider evolves a cocoon which limits a particular predator from gaining access to the eggs or spiderlings. In response, the predator evolves a means of circumventing the defense. The spider then counters the predators ability to circumvent the defense by evolving another defense or improving upon the first. Chapter VI indicates that cocoons do act as barriers to both generalist and specialist egg predators. However, many of the cocoon layers which function as barriers are not 100% effective in keeping out attackers, and in many cases this inability to totally limit predators is related to predator specialization (see also Austin, In press). It also

appears that the third criteria for coevolution, a counter-response by the spiders, has evolved in the form of larger clutches and thicker cocoon layers (Chapter VI), or temporal and spatial reproductive behaviors (Chapter VII). Caution should be invoked, however! The evidence presented here suggests that many of these behaviors did not evolve exclusively as counter-adaptations to specialized predators. For example, M. lemniscata shows a shift in reproduction to the early summer, and a compressed reproductive season, both of which limit the number of parasites available to attack the cocoons. However, these behaviors may also be the result of other factors, such as competition for prey with other orb-weavers in the habitat (Anderson 1978). Even more important is the duality of function displayed by many of the structural "adaptations" against predator attack. This suggests that in many cases, cocoons and their associated suspension systems probably represent responses to a wide variety of factors which are operating at the same time (diffuse evolutionary pressures), rather than from a response to one single factor such as predation or parasitism.

Conclusions

The results of this study demonstrate that the suspension system of M. lemniscata cocoons protects the eggs and spiderlings from drowning by keeping the cocoon off of the ground, keeps water from gaining access to the cocoon, and isolates the cocoon from generalist arboreal and terrestrial predators. It may also protect the eggs and spiderling from physical damage. The cover of

M. lemniscata cocoons protects the spiderlings from dessication and fungal attack, keeps water from entering the cocoons, and protects the eggs and spiderlings from predators. The cover may also provide some protection for the eggs and spiderlings from temperature extremes and physical damage.

The suspension system of A. aurantia cocoons protects the eggs and spiderlings by keeping water from the cocoon, isolates the cocoon from generalist arboreal and terrestrial predators, and inhibits oviposition by wasp predators. It may also provide some protection from physical damage. The cover of A. aurantia cocoons prevents water from entering the cocoon, creates a dead air space which acts as insulation, and protects the eggs and spiderlings from a number of specialized predators. The flocculent silk layer in A. aurantia cocoons is unwettable and may function to repel water. It also works to protect the eggs from predator attack and appears to function against wasp egg specialists. It may also play a role in protecting the eggs and spiderlings from physical damage and fungal attack.

These results, in combination with the few other studies on cocoon function (Schaefer 1976, Austin and Anderson 1978, Christenson and Wenzl 1980), suggest that the primary function of cocoons is probably to protect the eggs and spiderlings from predators and parasites. These studies also suggest that the time the eggs and spiderlings spend in the cocoon in diapause or overwintering has a strong influence on the strucure of the cocoon and should select for covered cocoons. Covered cocoons may also be

expected to be found among those spiders that suspend their cocoon because of the possibility of damage.

The results of this study point out, however, that interpretation of cocoon function is difficult because the various layers can perform one or more functions depending on the size of the egg mass, the morphology of the eggs, the ability of the eggs and spiderlings to control dessication, the habitat used for oviposition, and the number and kinds of predators in the habitat. The results also show that spiders use various reproductive behaviors resulting in spatial and temporal patterns of cocoon distribution that may aid in protecting the eggs and spiderlings by making cocoons difficult to locate. This study further suggests that eggs and spiderlings may be protected from pathogens by chemicals applied to cocoon covers. Finally, this study illustrates the need for further work in the area of cocoon architecture and function before the role of the cocoon and its place within the reproductive strategies of spiders can be fully understood.

LITERATURE CITED

Anderson, J.F. 1978. Energy content of spider eggs. Oecologia 37: 41-57.

Askew, R.R. 1971. Parasitic Insects. Heinemann Educational Books, London. 316 pp.

Austin, A.D. 1984. Life history of Clubiona robusta L. Koch and related species (Araneae, Clubionidae) in South Australia. J. Arachnol. 12: 87-104.

Austin, A.D. In press. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. J. Nat. Hist.

Austin, A.D., and D.T. Anderson. 1978. Reproduction and development of the spider Nephila edulis (Koch) (Araneidae: Araneae). Aust. J. Zool. 26: 501-518.

Auten, M. 1925. Insects associated with spider nests. Ann. Entomol. Soc. Amer. 18: 240-250.

Bijl, van der, P., and A. Paul. 1922. A fungus Gibbellula haygarthii n. sp. on a spider of the family Lycosidae. Trans. Roy. Soc. S. Africa 10: 149-150.

Bristowe, W.S. 1941. The Comity of Spiders. The Ray Society, London. 560 pp.

Brower, L.P., and J.V. Brower. 1972. Parallelism, convergence, divergence and the new concept of advergence in the evolution of mimicry. Trans. Connecticut Acad. Arts Sci. 44: 59-67.

Burks, B.D. 1979. Symphyta and Apocrita (Parasitica). Pages 990-1002 in K.V. Krombein, P.D. Hurd, Jr., D.R. Smith, and B.D. Burks, eds. Catalog of the Hymenoptera in America North of Mexico. I. Smithsonian Institution Press, Washington, D.C.

Champlain, A.B. 1922. Records of hymenopterous parasites in Pennsylvania. Pysche 29: 95-100.

Chapman, R.F. 1967. The Insects: Structure and Function. Elsevier North Holland, Inc., New York. 819 pp.

Chauvin, G., G. Vannier, and A. Gueguen. 1979. Larval case and water balance in Tinea pellionella. J. Insect Phys. 25: 615-619.

Christenson, T.E., and P.A. Wenzl. 1980. Egg laying of the Golden Silk Spider, Nephila clavipes L. (Araneae: Araneidae): Functional analysis of the egg sac. Anim. Behav. 28: 1110-1118.

Clark, P.J., and F.C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

Clark, P.J., and F.C. Evans. 1979. Generalization of a nearest neighbor measure of dispersion for use in K dimensions. Ecology 60: 316-317.

Coquillet, D.W. 1898. On the habits of the Oscinidae and Agromyzidae reared at the United States Department of Agriculture. U.S.D.A. Div. Ent. Bull. 10 (N.S.): 70-79.

Cresson, E.T. 1870. Descriptions of new species belonging to the sub-family Pimplariae found in America north of Mexico. Trans. Amer. Ent. Soc. 3: 145-148.

Davidson, A. 1896. Parasites of spider eggs. Entomol. News 7: 319-320.

Davies, M.E., and E.B. Edney. 1952. The evaporation of water from spiders. J. Exp. Biol. 29: 571-582.

Dawkins, R., and J.R. Krebs. 1979. Arms races between and within species. Proc. Royal Soc. Lond., B. 205: 489-511.

DeBach, P. 1944. Environmental contamination by an insect parasite and the effect on host selection. Ann. Entomol. Soc. Am. 37: 70-74.

Dethier, V.G. 1947. The response of hymenopterous parasites to chemical stimulation of the ovipositor. J. Exp. Zool. 105: 199-207.

Doutt, R.L. 1959. The biology of parasitic hymenoptera. Ann. Rev. Entomol. 4: 161-182.

Dowell, R.V. 1979. Effects of low host density on oviposition by larval parasitoids of the alfalfa weevil. J. N.Y. Entomol. Soc. 87: 9-14.

Eason R.R., W.B. Peck, and W.H. Whitcomb. 1967. Notes on spider parasites, including a reference list. J. Kansas Entomol. Soc. 40: 422-434.

Eberhard, W.G. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11: 292-300.

Edgar, W.D. 1971. Aspects of the ecology and energetics of the egg sac parasites of the wolf spider Pardosa lugubris (Walckenaer). Oecologia 7: 155-163.

Enders, F. 1974. Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. Ecology 55: 317-328.

Evans, R.E. 1969. Parasites of spiders and their eggs. Proc. Birmingham Nat. Hist. Soc. 21: 156-168.

Fisher, R.C. 1971. Aspects of the physiology of endoparasitic hymenoptera. Biol. Rev. 46: 243-278.

Flanders, S.E. 1953. Variation in susceptibility of citrus-infesting coccids to parasitization. J. Econom. Entomol. 46: 266-269.

Foelix, R.F. 1982. Biology of Spiders. Harvard University Press, Cambridge. 306 pp.

Free, C.A., J.R. Beddington, and J.H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. J. Anim. Ecol. 46: 543-554.

Fulton, B.B. 1933. Notes on Habrocytus cerealellae, parasite of the Angoumois grain moth. Ann. Entomol. Soc. Am. 26: 536-553.

Gertsch, W.J. 1979. American Spiders, 2nd Ed. D. van Nostrand Company, Inc., New York. 274 pp.

Gilbert, L.E. 1971. Butterfly-plant coevolution: Has Passiflora adenopoda won the selectional race with heliconiine butterflies? Science 172: 585-586.

Grim, J.N., and C.N. Slobodchikoff. 1978. Chorion surface features of some spider eggs. Pan-Pacific Entomol. 54: 319-322.

Grim, J.N., and C.N. Slobodchikoff. 1982. Spider egg chorion sphere size and density. Ann. Ent. Soc. Amer. 75: 330-334.

Hall, D.G. 1937. The North and Central American spider parasites of the genus Pseudogaurax (Diptera: Chloropidae). J. Wash. Acad. Sci. 27: 255-2261.

Hassell, M.P. 1966. Evaluation of parasite or predator responses. J. Anim. Ecol. 35: 65-75.

Hassell, M.P. 1971. Mutual interference between searching insect parasites. J. Anim. Ecol. 40: 473-486.

Hassell, M.P. 1978. The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton. 246 pp.

Hassell, M.P., and R.M. May. 1973. Stability in insect host-parasitoid models. J. Anim. Ecol. 42: 693-726.

Hassell, M.P., and R.M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol. 43: 567-594.

Heath, J.E. 1964. Reptilian thermoregulation: Evaluation of field studies. Science 146: 784-785.

Hickman, V.V. 1970. The biology of the Tasmanian Chloropidae (Diptera) whose larvae feed on spider's eggs. J. Entomol. Soc. Australia (N.S.W.) 7: 8-33.

Hieber, C.S. 1984. Egg predators of the cocoons of the spider Mecynogea lemniscata (Araneae: Araneidae): Rearing and population data. Florida Entomol. 67: 176-178.

Horner, N.V., and K.J. Starks. 1972. Bionomics of the jumping spider Metaphidippus galathea. Ann. Ent. Soc. Amer. 65: 602-607.

Howard, L.O. 1892. Hymenopterous parasites of spiders. Proc. Entomol. Soc. Washington 2: 290-303.

Humphreys, W.F. 1974. Behavioral thermoregulation in a wolf spider. Nature 251: 502-503.

Humphreys, W.F. 1983. The surface of spider's eggs. J. Zool. (London) 200: 305-316.

Jantzen, D.H. 1980. When is it coevolution? Evolution 34: 611-612.

Kaston, B.J. 1948. Spiders of Connecticut. State Geological and Natural History Survey No. 70, Hartford. 874 pp.

Kaston, B.J. 1970. Comparative biology of American black widow spiders. Trans. San Diego Soc. Nat. Hist. 16: 33-82.

Kaston, B.J., and G.E. Jenks. 1937. Dipterous parasites of spider eggs. Bull. Brooklyn Entomol. Soc. 32: 160-165.

Kaufman, W.C., D. Bothe, and S.D. Meyer. 1982. Thermal insulating capabilities of outdoor clothing materials. Science 215: 690-691.

Kessel, E.L., and B.B. Kessel. 1937. The life history of Gaurax araneae Coq., an egg predator of the black widow spider, Lactrodectus mactans (Fabr.). Pan-Pacific Entomol. 13: 58-60.

Kessler, A., and A. Fokkinga. 1973. Hymenopterous parasites in the egg sacs of spiders of the genus Pardosa (Araneida, Lycosidae). Tijdschr. Entomol. 116: 46-61.

Kirchner, W., and P. Kestler. 1969. Untesuchungen zur Kalteresistenz der Schilfradspinne Araneus cornutus (Araneidae). J. Insect Physiol. 15: 41-53.

Koebele, A. 1887. Some of the bred parasitic hymenoptera in the National Collection. Insect Life 3: 461.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford University Press, New York. 343 pp.

Lack, D. 1966. Population Studies of Birds. Oxford University Press, New York. 341 pp.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London. 409 pp.

Laing, J. 1937. Host-finding by insect parasites. I. Observations on the finding of hosts by Alysia manducator, Mormoniella vitripennis, and Trichogramma evanescens. J. Anim. Ecol. 6: 298-317.

Laing, J. 1938. Host-finding by insect parasites. II. The chance of Trichogramma evanescens finding its hosts. J. Exp. Biol. 15: 281-302.

Lees, A.D. 1947. Transpiration and the structure of the epicuticle in ticks. J. Exp. Biol. 23: 379-410.

Levi, H.W. 1968. The spider genera Gea and Argiope in America (Araneae: Araneidae). Bull. Mus. Comp. Zool. 136: 319-352.

Levi, H.W. 1980. The orb-weaver genus Mecynogea, the subfamily Metinae and the genera Pachygnatha, Glenognatha, and Azila of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). Bull. Mus. Comp. Zool. 149: 1-74.

Levi, H.W., and L.R. Levi. 1969. Eggcase construction and further observations on the sexual behavior of the spider Sicarius (Araneae: Sicariidae). Psyche 76: 29-40.

May, R.M. 1978. Host-parasitoid systems in patchy environments: A phenomenological model. J. Anim. Ecol. 47: 833-844.

McClure, M.S. 1977. Parasitism of the scale insect, Fiorinia externa (Homoptera: Diaspididae), by Aspidiotiphagus citrinus (Hymenoptera: Eulophidae), in a Hemlock forest: Density dependence. Environ. Entomol. 6: 551-555.

McCook, H.C. 1890. American spiders and their spinning work. II. Acad. Nat. Sci. Philadelphia. 479 pp.

McEwon, K.C. 1963. Australian Spiders. Sirius Books, Sydney. 287 pp.

Moore, C.W. 1977. The life cycle, habitat, and variation in selected web parameters in the spider Nephila clavipes Koch (Araneidae). Am. Midl. Nat. 98: 95-108.

Morrison, G., W.J. Lewis, and D.A. Nordlund. 1980. Spatial variations in Heliothis zea egg density and the intensity of parasitism by Trichogramma spp.: An experimental analysis. Environ. Entomol. 9: 79-85.

Morrison, G., and D.R. Strong. 1980. Spatial variations in host density and the intensity of parasitism: Some empirical examples. Environ. Entomol. 9: 149-152.

Mullen, G.R. 1969. Morphology and histology of the silk glands in Araneus sericatus Cl. Trans. Am. Microsc. Soc. 88: 232-240.

Muma, M.H., and K.J. Stone. 1971. Predation of Gastercantha cancriformis (Arachnida: Araneidae) eggs in Florida citrus orchards by Phalacrotophora epeirae (Insecta: Phoridae) and Arachnophaga ferruginea (Insecta: Eupelmidae). Florida Entomol. 54: 305-310.

Murdoch, W.W., and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9: 1-131.

Nellist, D.R. 1965. Some preliminary notes on the attack of spiders by fungi. Flatford Mill Spider Group. Bull. #26.

Norgaard, E. 1951. On the ecology of two Lycosid spiders (Pirata piraticus and Lycosa pullata) from a Danish Sphagnum bog. Oikos 3: 1-21.

Norgaard, E. 1956. Environment and behavior of Theridion saxatile. Oikos 37: 41-57.

Opell, B.D. 1984. Eggsac differences in the spider family Uloboridae (Arachnida: Araneae). Trans. Am. Microsc. Soc. 103: 122-129.

Peterson, A. 1964. Entomological Techniques. Edwards Brothers, Inc., Ann Arbor. 435 pp.

Prakash, R.N., and T.J. Pandian. 1978. Energy flow through dipteran parasite and hymenopteran hyperparasite populations. Oecologia 33: 209-219.

Price, P.W. 1970a. Trail odors: Recognition by insects parasitic on cocoons. Science 170: 546-547.

Price, P.W. 1970b. Biology of and host exploitation by Pleolophus indistinctus. Ann. Entomol. Soc. Am. 63: 1502-1509.

Price, P.W. 1980. Evolutionary Biology of Parasites. Monographs in Pop. Biol.#15. Princeton University Press, Princeton. 237 pp.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Redborg, K.E., and E.G. MacLeod. In press. The developmental ecology of Mantispa uhleri Banks (Neuroptera: Mantispidae). Illinois Biol. Monographs.

Reichert, S.E. 1981. The consequences of being territorial: Spiders, a case study. Am. Nat. 117: 871-892.

Reiskind, J. 1969. The spider subfamily Castianeirinae of North and Central America (Araneae, Clubionidae). Bull. Mus. Comp. Zool. 138: 163-325.

Riddle, W.A. 1981. Cold survival of Argiope aurantia spiderlings (Araneae, Araneidae). J. Arachnol. 9: 343-345.

Riddle, W.A., and A.L. Markezich. 1981. Thermal relations of respiration in the garden spider, Argiope aurantia, during early development and overwintering. Comp. Biochem. Physiol. 69A: 759-765.

Robinson, M.H. 1980. The ecology and behavior of tropical spiders. C.R. 8th Congr. Intern. Arachnol., Vienna: 13-32.

Robinson, M.H., and B. Robinson. 1976. The ecology and behavior of Nephila maculata: A supplement. Smith. Cont. Zool. 218: 1-22.

Salt, G. 1935. Experimental studies in insect parasitism. III. Host selection. Proc. Royal Soc. Lond., B. 117: 413-435.

Salt, G. 1937. The sense used by Tricogramma to distinguish between parasitized and unparasitized hosts. Proc. Royal Soc. Lond., B. 122: 57-75.

Schaefer, M. 1976. An analysis of diapause and resistance in the egg stage of Floronia bucculenta (Araneae: Linyphiidae). Oecologia 25: 155-174.

Schaefer, M. 1977. Winter ecology of spiders (Araneida). Z. Ang. Ent. 83: 113-134.

Scheffer, T.H. 1905. The cocooning habitats of spiders. Kansas Univ. Sci. Bull. 3: 85-114.

Schildknecht, H., P. Kunzelmann, D. Krauss, and C. Kuhn. 1972. Uber die Chemie der Spinnwebe, I. Arthropodenabwehrstoffe. Naturwissenschaften 59: 98-99.

Schoener, T. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Sys. 2: 369-404.

Seligy, V.L. 1971. Postembryonic development of the spider Enoplagnatha ovata (Theridiidae). Zool. J. Linn. Soc. 50: 21-31.

Sokal R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Company, San Francisco. 776 pp.

Stiling, P.D., and D.R. Strong. 1982. Egg density and the intensity of parasitism in Prokelisia marginata (Homoptera: Delphacidae). Ecology 63: 1630-1635.

Tolbert, W.W. 1976. Population dynamics of the orb weaving spiders Argiope trifasciata and Argiope aurantia (Araneae, Araneidae): Density changes associated with mortality, natality, and migrations. Ph.D. dissertation, University of Tennessee, Knoxville. 172 pp.

Tolbert, W.W. 1979. Thermal stress of the orb-weaving spider Argiope aurantia (Araneae). Oikos 32: 386-392.

Trail, D.S. 1980. Predation by Argyrodes (Theridiidae) on solitary and communal spiders. Psyche 87: 349-355.

Turnbull, A.L. 1973. Ecology of the true spiders (Araneomorphae). Ann. Rev. Ent. 18: 305-348.

Varley, G.C. 1941. On the search for hosts and the egg distribution of some Chalcid parasites of the Knapweed Gall-Fly. Parasitology 33: 47-66.

Vinson, B.S. 1972. Competition and host discrimination between two species of tobacco budworm parasitoids. Ann. Entomol. Soc. Am. 65: 229-236.

Vinson, B.S. 1975. Biochemical coevolution between parasitoids and their hosts. Pages 14-36 in P.W. Price, ed. Evolutionary Strategies of Parasitic Insects and Mites. Plenum Press, New York.

Vinson, B.S. 1976. Host selection by insect parasitoids. Ann. Rev. Entomol. 21: 109-133.

Waage, J.K. 1979. Foraging for patchily-distributed hosts by the parasitoid, Nemeritis canescens (Grv.). J. Anim. Ecol. 48: 353-371.

Washburn, J.O., and H.V. Cornell. 1979. Chalcid parasitoid attack on a gall wasp population (Acraspis hirta (Hymenoptera: Cynipidae)) on Quercus prinus (Fagaceae). Can. Entomol. 111: 391-400.

Winston, P.W., and D.H. Bates. 1960. Saturated solutions for the control of humidity in biological research. Ecology 41: 232-237.

Wise, D.H. 1982. Predation by the commensal spider, Argyrodes trigonum, upon its host: An experimental study. J. Arachnol. 10: 111-116.

Witt, P.N. 1971. Instructions for working with web-building spiders in the laboratory. Bioscience 21: 23-25.

Witt, P.N., C.F. Reed, and D.B. Peakall. 1968. A Spider's Web. Springer-Verlag, Inc., New York. 107 pp.

Yoshikura, M. 1969. Effects of UV irradiation on the embryonic development of a liphistiid spider, Heptathela kinmura. Kumamuto J. Sci., B. 2: 57-108.

Zar, J.H. 1984. Biostatistical Analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs. 718 pp.

BIOGRAPHICAL SKETCH

Craig Stephen Hieber was born into the midst of the urban-industrial wasteland in East Orange, New Jersey in 1951. At age 15, after constant exposure to New York city television and radio, he moved to Chester, in northern New Jersey, where he attended West Morris High School. After graduation from high school in 1969, he studied mechanical engineering at the University of Virginia for 2 years. In 1975, he received a B.S. in biology from Roanoke College. He then moved to Vermont where there were no jobs but the scenery was beautiful. From Vermont, he moved to North Dakota where he received an M.S. in biology in 1979 from the University of North Dakota. After three years of -20 degree winters, he moved to Florida where he expects to receive a Ph.D. in zoology in 1984 from the University of Florida. When he is not studying the behavioral or physiological ecology of insects and spiders, he devotes most of his time to general tool use, the restoration of machinery and furniture, tropical fish, and his passion, bicycles.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Anderson, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Lincoln P. Brower
Distinguished Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Jonathon Reiskind
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Reese I. Sailer
Graduate Research Professor of
Entomology and Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Arts and Sciences and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1984

_____

Dean for Graduate Studies and Research